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POPULATION CHARACTERISTICS OF *ESCHSCHOLZIA RHOMBIPETALA* (PAPAVERACEAE)

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Abstract

A population of *Eschscholzia rhombipetala,* a species that, until several years ago, was thought to be extinct, occurs in and around a hillside slump (small landslide) in the Corral Hollow area of the Altamont Hills of California. Here we describe the population and co-occurring vegetation from a five-year study. A second population was found fewer than 3 km away from this population in spring of 2002. Where possible, data from both populations are reported. Both populations occur on clay soil like the only other known population in the Carrizo Plain. Population numbers ranged from 9 to 285 plants. *Eschscholzia rhombipetala* presence was negatively correlated with exotic grass and thatch cover and positively correlated with bare ground and exotic forb cover. Plant height predicted number of reproductive units (buds plus flowers plus seed capsules) per plant ($P < 0.004$) and seed capsule length was also highly correlated with plant height ($P < 0.001$). Plant performance was significantly different among microhabitats, and plants in the active slump tended to do better than those elsewhere. The population expansion upslope into grassland areas in 2002 may indicate the presence of a seed bank for this small-seeded annual, and its association with bare ground and greater performance in the slump may indicate that some disturbance is necessary for population maintenance.

Key Words: *Eschscholzia rhombipetala,* rare plants, disturbance, clay soils, California grassland.

Eschscholzia rhombipetala (the diamond-petaled poppy, E. Greene) is an extremely rare spring-flowering annual plant included on the California Native Plant Society (CNPS) List 1B (CNPS 2001). The historic range of this species includes the inner north Coast ranges, the eastern San Francisco Bay region, and the inner South Coast Ranges. The last herbarium collections of this plant were made in 1950 in San Luis Obispo county, and the species has since been presumed extinct. In 1993, a population of *E. rhombipetala* was discovered in the northern part of the Carrizo Plain by David Keil (personal communication) of California Polytechnic University, San Luis Obispo, but has not been seen since 1995.

A population of *E. rhombipetala* was identified during a habitat survey in 1997 at Site 300 (Preston 2000), a high-explosive test site operated by the University of California for the Department of Energy in the Corral Hollow area, on the border between Alameda and San Joaquin counties (Fig. 1). The 13-hectare site is closed to the public and has had no agricultural activities since its establishment in the 1950's. Collections of *E. rhombipetala* have been made at Corral Hollow, both in 1937 (UC765993) and in 1949 (P. Raven personal communication). Like the Carrizo plain population, the first Site 300 *E. rhombipetala* population occurs in an ecotone on heavy clay soil. The ecotone at Site

300 was formed by a landslide within a minor east-west drainage to a major north-south trending canyon. The landslide formed a slump at the bottom of the slide, with sharp scarp faces on the northern and southern sides of the slump. This *E. rhombipetala* population is found on the southern side of the slump (a north-west facing aspect) near the edge of the scarp, some distance into the surrounding grassland, and in the slump itself. The slump and surrounding grasslands are composed primarily of exotic species in the genera *Avena, Bromus, Sonchus* and *Brassica.* The rare tarplant *Blepharizonia plumosa* (CNPS List 1B, CNPS 2001) and its more common relative *Blepharizonia laxa* (Baldwin et al. 2001) also occur in the slump.

A second population of *E. rhombipetala* was discovered in spring of 2002 in another habitat survey, less than three km from the first population (location1). This population occurs on a steep, north-west-facing slope. While it may occur on an historic slump, the soil of the population area is not noticeably more active than its surroundings. The second population at location 2 occurs in a grassland of exotic species similar to that at location 1.

Eschscholzia rhombipetala is a small (5–30 cm tall), erect annual. It is similar in appearance to other *Eschscholzia* species, but is quite diminutive and easily overlooked. The yellow petals are 3–15 mm long on a barrel-shaped receptacle, and when in bud, may be erect or nodding, with a blunt or short point. The fruit is a capsule, generally 4–7 cm long, containing numerous round, net-ridged black seeds 1.3–1.8 mm wide (Clark 1993).

In this paper we describe the *E. rhombipetala*

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Fig. 1. General location of Site 300 in the Corral Hollow area of California.

population and the vegetation surrounding it. Through this research, we hope to describe the population, eventually predict circumstances under which large population sizes may be found, and aid other researchers in locating additional populations of this rare plant species.

Materials and Methods

Census

The entire *E. rhombipetala* population at location 1 was censused on 08 Apr 98. Small, numbered flags were used to mark individual plants so they could be tracked. Height, flower number, capsule number and capsule length data were collected. On 18 Apr 98, the population was revisited and marked plants were found and remeasured. The same method of measuring and marking took place on 30 Apr 99, with a follow-up visit on 21 May 99. In 2000 through 2002, the population was censused on single dates: 24 Mar 00, 30 Mar 01, and 29 Mar 02. The population at location 2 was censused on 05 Apr 02. Data collected for marked and measured plants were height, flower number, capsule number and capsule lengths. During the 2000–2002 censuses, the geographic features of the slump (SL), within 50 cm of the scarp next to the slump (SC), or in the interior grassland (GR), was recorded for all plants in the location 1 population.

Linear regression was performed using PROC GLM in SAS (SAS 1990) to examine the relationship between plant height and number of floral units (buds + flowers + capsules) and capsule length. Tukey's separation of means was performed to determine the effect of geographic feature on the number of floral units (Steel et al. 1997).

Vegetation Sampling

On 21 May 99 and 27 Apr 00, cover and composition of species in the *E. rhombipetala* population area were recorded at location 1. On 30 Mar 01, 34 plots were located to cover the entire *E. rhombipetala* population, and 25 plots were randomly located outside the population. For each plot, species were identified and their percent cover was visually estimated. Percent bare ground and percent thatch cover were also recorded. Areas with differing dominant species were also mapped in and around the slump. In 2002, cover data were collected from 63 plots at location 1 on 29 Mar (31 in the *E. rhombipetala* population and 32 outside it) and 30 plots at location 2 on 5 Apr (14 within the population and 16 outside it) using the same methodology.

Logistic regression using PROC LOGISTIC in SAS version 6.0 (SAS 1990) was performed to determine effects of vegetation on *E. rhombipetala* presence/absence. Due to missing data points, only 144 plots were analyzed. The logistic regression model was $p/(1 - p) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n$, where p is the probability of *E. rhombipetala* presence in the plot, α is the intercept, β is the parameter estimate, and x is the covariate. Bare ground, thatch, exotic grass, native grass, exotic forb, and native forb covers were used as covariates. When the parameter estimate is negative, the covariate is negatively associated with *E. rhombipetala* presence.

Soil Sampling

Soil samples were collected from both locations on 08 May 02. Location 1 was divided into three sub-areas based on the geographic feature defined above (SL, SC, GR). Soil samples were collected from two locations in each sub-area, visually selected to be representative of the sub-area. Location 2 was not subdivided. Soil samples were collected from three locations, visually selected to be representative of site. At each sampling location, surface vegetation was scraped away with a trowel. The top 15 cm of soil in an approximately 30-cm^2 area was manually homogenized using the trowel. Soil samples were submitted to A&L Western Agricultural Laboratories in Modesto, California. Samples were analyzed for organic matter, nitrogen compounds (nitrate, ammonia, and total kjedhal nitrogen), sodium bicarbonate phosphorus, extractable cations, hydrogen, pH, cation exchange capacity, soluble salts, sulfate sulfur, zinc, manganese, iron, copper, boron and soil texture using standard agricultural methods as outlined in the North American Proficiency Testing Program and the USDA (Neufeld and Davison 2000).

Results

Census

The *E. rhombipetala* population at location 1 comprised 24 plants in 1998 (Table 1), 9 plants in

TABLE 1. HEIGHT, NUMBER OF FLORAL UNITS (BUDS + FLOWERS + CAPSULES) PER PLANT, AND CAPSULE LENGTH FOR MARKED *E. RHOMBIPETALA* PLANTS: 1998–2002. All averages are ± one standard deviation. [a] Number of plants measured is the same for the height and number of flowers measurement. Plants with no flowers were included in the average. [b] Number of plants measured for capsule length includes only those plants with capsules.

Location	Date measured	Height (cm)	# floral units/plant	N[a]	Capsule length (cm)	N[b]
1	18 Apr 98	7.5 ± 2.8	0.4 ± 0.5	24	2.8 ± 1.4	16
1	30 Apr 99	6.0 ± 1.8	0.7 ± 0.7	9	2.1 ± 0.6	6
1	24 Mar 00	5.5 ± 2.1	0.6 ± 0.5	171	2.3 ± 1.4	44
1	30 Mar 01	5.0 ± 2.5	0.3 ± 0.5	189	2.8 ± 1.8	72
1	29 Mar 02	6.8 ± 2.5	1.1 ± 0.7	280	3.4 ± 1.6	73
2	05 Apr 02	8.0 ± 2.1	1.4 ± 0.7	76	3.3 ± 0.3	63

1999, 273 plants in 2000 (171 were marked and measured), 189 plants in 2001, and 285 plants in 2002 (280 were marked and measured). The location 2 population contained 76 plants in 2002. The three-week monitoring period of 1999 resulted in a recorded 67% survivorship. Two plants died in the 10 days prior to the 1998 full census. In both years, deaths occurred in well-established vegetative individuals. All dead plants wilted without flowering, apparently due to the shifting of soil within the slump. No survivorship data were recorded for 2000 through 2002. Plants were small, with average heights ranging from 5.0 ± 2.5 to 8.0 ± 2.1 cm (Table 1). Plants as short as 2.5 cm were observed flowering and the largest plants recorded were approximately 14 cm tall. Most plants had only one flower open at a time, but senescent plants usually had several capsules per plant.

There was a significant positive relationship between plant height and number of floral units (buds + flowers + capsules) as well as between plant height and capsule length at location 1. Data were too few in 1999 to perform regression. In 1998, 2000 and 2001 slopes ranged from 0.09 to 0.19 and intercepts ranged from 0.08 to −0.17 (P < 0.003, r^2 = 0.22 to 0.33). In 2002, more plants had floral units compared to other years, and the average number of floral units per plant was greater than one for the first time; the slope of the regression was 1.4, and the intercept was 5.2 (P < 0.001, r^2 = 0.14). Plant height was not a significant predictor of the number of floral units at location 2 (P > 0.05).

Plant height was even more closely tied to capsule length variation. Again, in 1998, 2000 and 2001, slopes were low (0.35 to 0.48), intercepts were small (−1 to −0.1), and r^2 was high (0.44 to 0.66, P < 0.001). In 2002, capsule lengths were longer than they had been in previous years. In 2002, height explained over 20% of capsule length variation at both location 1 and location 2, and this was a year where the regression intercept was high (5.5 and 5.3 respectively) and the slope of the line was larger (0.94 and 0.89 respectively, P < 0.001).

Geographic feature had an effect on plant performance. In 2002, plants had the most floral units at location 2 and in the slump at location 1 (Fig. 2; P < 0.05). Plants in the slump generally performed well, either with the most floral units per plant (in 2000 and 2002), or with no significant difference between them and the best performers (which were plants in the grassland in 2001). The slump contained anywhere from 42% to 24% of the total plants in the location 1 population. Plants at location 2, even though they were located in a grassland area without an active slump, performed as well as plants in the slump at location 1 in the year when both locations were monitored.

Vegetation Sampling

In 1999 and 2000, *Avena* sp. and *Bromus diandrus* were the dominant species in almost all of the areas at location 1. The slump itself had an extremely large bare ground component that would not be repeated in succeeding years. The *E. rhombipetala* population was concentrated in one corner of the slump and adjacent grassland. The *E. rhombipetala* population expanded downslope in 2000 to double its population area. In 2001, the *E. rhombipetala* population expanded northward across the slope into the scarp. *Bromus* species were more mixed in 2001, and large areas of *Avena* sp. included a substantial forb component. *Poa secunda* became dominant in the scarp and the slump in 2001. In 2002, most of the vegetation patterns were similar to those in 2001, with the *E. rhombipetala* population expanding into the grassland areas upslope of the slump. *Lupinus microcarpus* became quite evident in the southern scarp and grassland in 2002. Table 2 shows plants that occurred in and around the *E. rhombipetala* populations of both locations.

Logistic regression showed that bare ground, thatch cover, exotic grass and exotic forb cover were important for predicting *E. rhombipetala* presence (Table 3). Percent bare ground, percent thatch cover, percent exotic grass cover, and percent exotic forb cover all contributed significantly to the model (P ≤ 0.007). Native grass and native forb cover did not contribute significantly to the prediction of *E. rhombipetala* presence. As thatch cover and exotic grass cover increase, the likelihood of *E. rhombipetala* presence decreases. Probability of *E. rhombipetala* presence increases as exotic forb cover and
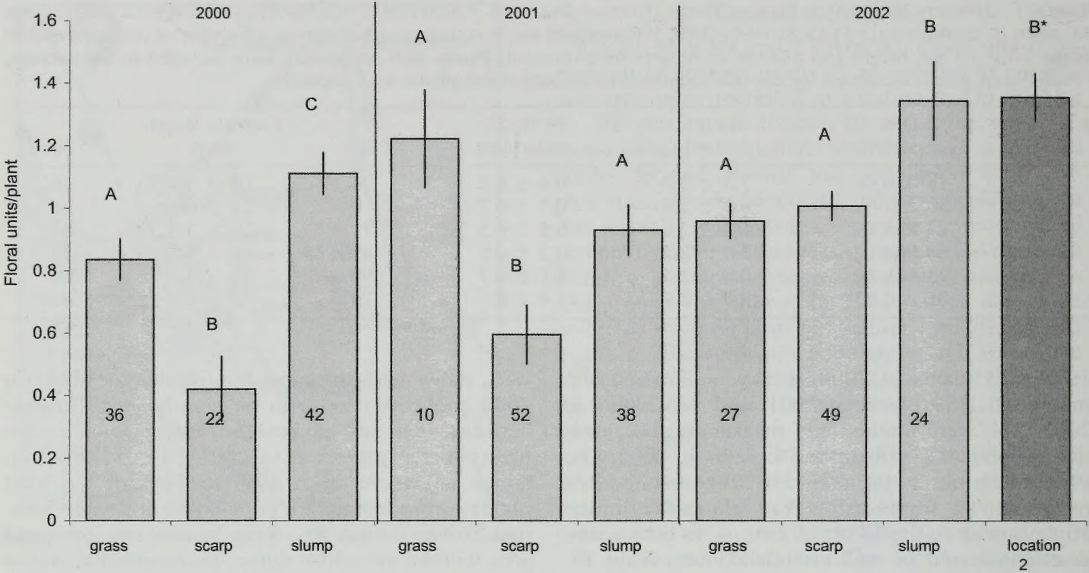
FIG. 2. Number of floral units per plant by site at location 1 in 2000–2002 and at location 2 in 2002. All bars are one standard error. Different letters indicate significant differences (P < 0.05) among sites within years. Numbers inside bars indicate the percent of plants found at each site in location 1. *Location 2 also different from location 1 when all location 1 sites are lumped.

TABLE 2. PLANT SPECIES FOUND IN AND AROUND *E. RHOM-BIPETALA* POPULATIONS. For plants identified only to genus, native versus exotic identifications were made using species lists generated by Taylor and Davilla (1986).

Native	Exotic
Grasses	
Elymus sp.	*Avena* sp.
Poa secunda	*Bromus diandrus*
	Bromus hordeaceous
	Bromus madritensis subsp. *rubens*
	Hordeum murinum
	Vulpia myuros
Forbs	
Amsinckia intermedia	*Brassica* sp.
Amsinckia mensezii	*Carduus pynocephalus*
Blepharizonia laxa	*Centaurea melitensis*
Blepharizonia plumosa	*Erodium cicutarium*
Brodiaea sp.	*Medicago polymorpha*
Claytonia parviflora	*Salsola tragus*
Dichelostema capitatum	*Sanicula bipinnata*
Eschscholzia rhombipetala	*Sonchus* sp.
Galium aparine	
Gutierrezia california	
Lepidium nitidum	
Lotus wrangellianus	
Lupinus microcarpus	
Monolopia major	
Stylomecon heterophylla	
Trifolium sp.	

percent bare ground increase. Plots with *E. rhombipetala* averaged 45% bare ground cover compared to 20% bare ground in plots without *E. rhombipetala* (Table 4). Thatch cover was 39% in plots without *E. rhombipetala* and 14% in plots with *E. rhombipetala*. Exotic grass cover was 20% in plots with *E. rhombipetala* and 27% in plots where *E. rhombipetala* was absent. Exotic forb cover averaged 6% in plots with *E. rhombipetala* and 3.5% in plots without *E. rhombipetala*.

Soil Sampling

Soils at locations 1 and 2 were clays and clay loams (Table 5). Soil nutrients were within the normal range of soils in the Altamont hills (data not shown, Webster-Scholten 1994), but nitrogen and ammonia are relatively low (Table 5). In California coastal grasslands, heavily disturbed soils have been shown to be low in nitrogen (Stromberg and Griffin 1996).

DISCUSSION

It is unclear whether these populations at Site 300 were present at the time the species was determined to be extinct. These populations occur away from regular Site 300 activities and may have been continuously present as aboveground plants. Alternatively, they may have been briefly extirpated and then rediscovered when the populations reappeared due to soil turnover or a long-range dispersal event. Long-distance dispersal events are rare, and it is not easy to confirm the extinction of plants that have

TABLE 3. RESULTS OF THE LOGISTIC REGRESSION: THE EFFECT OF VEGETATION ON *E. RHOMBIPETALA* ABSENCE. [a] Model fit (Wald) $P < 0.01$, $n = 149$ (69 plots with no *E. rhombipetala*, 75 plots with *E. rhombipetala*). The model is $P/(1 - P) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n x_n$ where P is the probability of *E. rhombipetala* absence from the plot, α is the intercept, β is the parameter estimate, and x is the covariate. In the model, bare ground, thatch, exotic grass, native grass, exotic forb, and native forb covers were used as covariates. [b] Odds ratio is probability *E. rhombipetala* present : probability *E. rhombipetala* absent.

Covariate x	P-value	β[a]	Odds ratio[b]	Confidence interval	Maximum measured x value[a]
Intercept $\alpha = -0.67$	0.411				
% bare ground	<0.001	0.046	1.047	1.021–1.074	80
% thatch cover	<0.001	−0.053	0.948	0.919–0.978	80
% exotic grass cover	<0.001	−0.058	0.944	0.906–0.984	70
% native grass cover	0.912	−0.004	0.996	0.919–1.078	40
% exotic forb cover	0.007	0.151	1.163	1.043–1.297	20
% native forb cover	0.990	−0.001	0.999	0.838–1.190	12.5

seed banks (Wolf 2001). A long-term seed bank or even continuously present aboveground plants are more likely explanations of the existence of these populations than a recent dispersal event.

Our yearly census of *E. rhombipetala* showed a wide range in population size, from a low of 9 to a high of 285 individuals. Fluctuation in the size of small, annual plant populations is to be expected (Parsons and Zedler 1997; Pavlik and Espeland 1998), but populations at both locations are still quite small. Although the nine plants observed at location 1 in 1999 may have produced enough seed to generate a population of 171 plants the following year, the 2002 appearance of plants upslope from where plants had been previously observed may indicate the presence of a seed bank for this population.

Reproductive success (number of floral units or capsule length) is better predicted from plant height in poor years than in good ones: the least predictive power came from regressions with very large intercepts, indicating that in a year like 2002 many of the smallest plants are able to put as much toward reproduction as the largest plants. Reproductive success was more strongly tied to plant height in years that were less favorable to *E. rhombipetala*. Small plants did less well relative to large plants in these poorer years with smaller population numbers. Although the year with the largest population size was also the year with the greatest small plant fitness, it is not clear at this time if these two factors are related.

The positive association of *E. rhombipetala* presence with bare ground, plus the better perfor-

mance of plants in the active slump may indicate that some level of disturbance is necessary for plants of this species to do well. Plants were negatively associated with high levels of thatch and exotic grasses. Thatch indicates an area that has not been disturbed (Stromberg and Griffin 1996), and an undisturbed environment is more likely to lead to the dominance of exotic grasses such as *Bromus diandrus* and *Avena* sp. (Brown and Bugg 2001). The negative relationship between thatch and exotic grasses and *E. rhombipetala* may be due to either microhabitat preference or to an inability on the part of *E. rhombipetala* to compete with exotic annual grasses. Further observations of the population at location 2, where there is no obvious disturbance like the slump at location 1, may shed additional light on the nature of this possible relationship.

Populations of *E. rhombipetala* observed within the last decade have occurred on soils with a clay component. At the Carrizo Plain location, *E. rhombipetala* grows on heavy clay soils that accumulate water in the spring, forming vernal pools. The population is located in an ecotone on the higher areas between an *Amsinckia*-dominated mound and a *Layia*-dominated swale, in open patches. The plants are an understory to taller *Lasthenia, Phacelia*, and various grasses (D. Keil personal communication). Both population locations in the Altamont hills can be characterized as occurring on clay or clay loam soils. It is possible the species may occur in more locations than previously thought, as other surveys for this plant have focused on more gravelly soils (C. Clark personal communication). Clay soils can

TABLE 4. VEGETATION CHARACTERISTICS OF PLOTS WITH AND WITHOUT *E. RHOMBIPETALA*. All values are averages ± one standard deviation.

Plot type	% bare ground	% thatch cover	% exotic grass cover	% native grass cover	% exotic forb cover	% native forb cover	N
No *E. rhombipetala*	19.6 ± 15.5	38.7 ± 25.2	27.0 ± 11.8	2.1 ± 6.1	3.5 ± 4.3	2.2 ± 3.0	69
With *E. rhombipetala*	44.9 ± 27.0	13.9 ± 14.0	20.3 ± 11.4	2.8 ± 6.0	6.1 ± 5.0	2.8 ± 3.4	75

TABLE 5. CHARACTERISTICS OF SOIL COLLECTIONS AND THEIR LOCATIONS. [a] Nitrate nitrogen (ppm). [b] Ammonia nitrogen (ppm).

Location	Slope	Aspect	Sand %	Silt %	Clay %	Soil type	NO3-N[a]	NH4-N[b]
Location 1								
Slump	32°	W	20.0 (1.4)	36.0 (4.2)	44.0 (2.8)	clay	6.5 (0.7)	<2.5
Scarp	42°	N	31.0 (5.7)	31.0 (0.0)	38.0 (5.7)	clay loam	6.5 (0.7)	3.1 (0.8)
Grassland	31°	NW	37.5 (14.8)	30.0 (1.4)	35.0 (12.7)	clay loam	6.0 (0.0)	<2.5
Location 2	32°	NW	33.7 (2.3)	23.0 (0.0)	43.3 (2.3)	clay	5.3 (0.6)	2.5 (0.0)

resist compaction through natural wetting and drying cycles (Ahmad 1993), and this attribute may be important for *E. rhombipetala* germination and growth. The low nitrogen levels in the soils may prevent overdominance of exotic annual grasses (Brown and Bugg 2001), which may also encourage *E. rhombipetala* persistence.

Eschscholzia rhombipetala is a small-seeded plant, and as such, may be dependent on soil turnover to return banked seeds up to germinable depths. Small seeds buried too deeply in the soil are unable to germinate into seedlings (Zhan and Maun 1994). It is likely that this species has a long-lived seed bank: studies of a small-seeded plant on serpentine clays showed that, for that species, seeds remained viable in the soil for more than eight years (Pavlik and Espeland 1998). Germination and early growth is more important than later life history stages for many California native forbs (Brown and Bugg 2001), and it is likely that the importance of these early life stages is even greater for those species with small seeds, which have fewer seed resources to overcome such hardships as limited light availability at early growth stages.

This paper is the first step in documenting the habitat associations and population dynamics of this extremely rare California annual plant. While we have been unable to rigorously determine factors important to *E. rhombipetala* plant fitness, we have found some indication that there is a positive relationship between *E. rhombipetala* and factors related to disturbance. We have found that the strength of the relationship of plant size to reproductive output changes among years and that in some years many small plants can have fairly high fitness. Continuing yearly population censuses will help us to determine factors that influence greater plant fitness and higher population sizes at the two locations reported on in this study. We hope that the research presented here will assist other botanists in locating additional populations of this plant.

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IMPACTS OF LIVESTOCK AND BURNING ON THE SPATIAL PATTERNS OF THE GRASS *NASSELLA PULCHRA* (POACEAE)

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Abstract

Knowledge of the response of native perennial plants to disturbances such as burning and grazing is needed for effective restoration and management. Spatial patterns of the perennial grass *Nassella pulchra* were analyzed following cessation of livestock grazing, continued moderate grazing, burning, and combined burning and grazing. Small-scale plant patterns on each site were analyzed using Ripley's K-function on the centers of occupied quadrats arranged on a square grid within 0.25 m^2 plots. *Nassella pulchra* distributions show that the burning treatment significantly increased the clump size from 12.0 to 16.7 cm (P = 0.03) and the grazing treatment decreased the clump size from 16.1 to 12.6 cm (P = 0.05). There was no significant interaction between burning and grazing (P = 0.49). Analysis of the observed frequencies within plots showed that the distribution of plants in the grazed treatment was more heterogeneous than the others (P = 0.08). The burning treatment analysis at this scale shows no effects (P = 0.81), and there was no significant interaction between burning and grazing (P = 0.78) or reduction in variance from the blocks (P = 0.36). This analysis reflects the increased heterogeneous distribution of *N. pulchra* at the 65 m^2 scale. Our results on plant distributions support the recommendation that *N. pulchra* responds well to burning and grazing exclusion. Determining the spatial and biological responses of species within the plant community structure is important if a species, such as *N. pulchra,* is to be the target of successful management.

Key Words: Purple needlegrass, coastal prairie, pattern analysis, native perennial grasses.

California's Mediterranean type grasslands are well suited for the study of how perennial grasses react to disturbance. Where present, the native perennials are surrounded by introduced annual species that have spread widely since the mid-1800's (Bartolome et al. 1986; Heady et al. 1991). *Nassella pulchra* (A. Hitchc.) Barkworth (purple needlegrass; nomenclature per Hickman 1993), California's most widespread native bunchgrass, is considered tolerant of moderate grazing (Bartolome and Gemmill 1981; Edwards 1995) and dry season (summer and fall) fires (Heady 1958), but may decline with heavy livestock use (Heady et al. 1991) or competition with exotic species (Bartolome and Gemmill 1981). Removal of livestock does not typically result in succession to a native dominated community. Even with heavy livestock grazing, some native perennial grasses are typically present (Heady et al. 1991), especially on coastal sites that have never been tilled (Stromberg and Griffin 1996).

While the historical addition of livestock and the corresponding increased grazing intensity may have reduced the native perennial grasses, they were also affected by changes in fire frequency (Burcham 1957). Greenlee and Langheim (1990) estimated that the fire frequency in the Monterey Bay area of California before the mid 1880's was 1–15 yr while after that time burning has only occurred every 20–30 yr. *Nassella pulchra* may be adapted to burning as Ahmed (1983) found that basal area increased significantly in burned plots compared to controls. Burning has also been advocated as a management tool for native perennial grass restoration in California (Menke 1982) and elsewhere (Axelrod 1985). Even though their genesis and management history are often unclear, areas with substantial cover of native perennials are often the target of conservation or enhancement efforts and a goal for restoration.

Analysis of spatial patterns in patches dominated by perennials should improve the formulation of hypotheses and help identify processes important for predicting plant responses to management. Previous work has shown that the quantitative description of a plant community's spatial structure can allow insight into such processes as community dynamics (e.g., Bolker and Pacala 1999), competition for resources (e.g., Martens et al. 1997) and plant correlation with environmental heterogeneity (e.g., Thompson et al. 1996). Grazing has a strong impact on the spatial patterns of perennial grasses in the Great Plains (Adler and Lauenroth 2000) and influences the spatial heterogeneity of many types of

ecosystems (Adler et al. 2001). Earlier analyses of a Californian coastal grassland (Hatch et al. 1999) found that changes in foliar cover associated with disturbance (burning/grazing) were not well coupled to changes in the density of plants, suggesting that spatial distributions of *N. pulchra* might have changed due to the burning and grazing treatments. Our objective was to evaluate the effects of fall burning and excluding grazing on spatial patterns of *N. pulchra* in a historically grazed Coastal Prairie of California. We hypothesized that disturbances (burning and/or grazing) would change the distribution of this native perennial grass.

METHODS

Study site and treatments. Pompanio Beach State Park is a coastal terrace with elevations ranging from sea level to 150 m. The park has a westerly exposure and is approximately 60 km south of San Francisco (37.42°N, 122.43°W). It is dominated by the historically important native-perennial grasses: *Nassella pulchra* and *lepida* (A. Hitchc.) Barkworth and *Danthonia californica* Bolander (Baker 1978). Slopes average 20%, rainfall averages 60 to 70 cm annually (with the majority falling in winter) and summer drought is moderated by frequent fog. Moderate (half or less of the forage was used) year-round livestock grazing has been conducted for at least the last 30 yr. Before that time, heavy grazing may have occurred episodically. During the study, the area exclusive of experimental exclosures was grazed by approximately 15 dairy cows and 200 sheep. The study plots were in a section of the park seldom grazed by cattle and unevenly grazed by sheep. The soils are fine, montmorillontic, thermic mollic palexeralfs (Tierra Loam) and fine-loamy, mixed, mesic typic argixerolls (Colma Sandy Loam; Wagner and Nelson 1961). Three blocks of approximately 0.25 ha each were established in native perennial stands on the upper, middle and lower slope of the park (Hatch et al. 1999). Fences constructed in late summer 1989 excluded livestock from the ungrazed treatments. The burning treatment was applied in November 1990, which is within the summer-fall historical period of natural fire in the region and precedes the late fall through spring growing season. Treatments were the factorial combinations of burning and grazing and randomly allocated on each of three blocks, providing three replications of about 65 m^2 each. All data were collected in 1991.

Plant biology. Nassella pulchra, a native perennial bunchgrass, is a prolific seed producing species (Sampson and Chase 1927; Dyer et al. 1996) and may establish from this sexually produced (amphimictic) outcrossing seed (Sampson and Chase 1927; Baker 1978). The seeds are of relatively high mass (4.88 mgs; Blumler 1992) compared to other common plants found on the park. The seeds have a long (7 to 9 cm) awn (Hitchcock 1950) and dis-

articulate readily. The inflorescent culms are erect and from 18 to 60 cm tall (Hickman 1993). The plant grows in bunches or tufts (Sampson and Chase 1927; Hitchcock 1950; Hickman 1993) with average basal areas observed as high as 129 cm^2 (White 1967). *Nassella pulchra* spreads vegetatively and breaks into independent ramets, especially when subjected to mechanical disturbance (Dyer et al. 1996). Vegetative parts of the same plant have been noted up to 30 cm apart (Hull and Muller 1975). It is unknown if the primary means of colonization of this species is by vegetative propagation or recruitment from seed. Mature plants may live 25 yr or more (Stromberg and Griffin 1996).

Sampling methods. Spatial pattern sampling involved placing a grid of 100 quadrats 25 cm^2 (5 × 5 cm) within 0.25 m^2 plots (50 × 50 cm). We recorded the presence of any *Nassella pulchra* plant with at least one aboveground part located within and rooted within a quadrat. The 0.25 m^2 grids were allocated at random by treatment replication, within areas dominated by perennial grasses (*see* Hatch et al. 1999). A total of 96 plots were sampled (eight per replication, *see* Fig. 1) but due to analysis constraints (discussed later) the unburned-ungrazed treatment combination was represented by one, three and three plots per block, unburned-grazed by two, zero and four plots, burned-ungrazed by four, two and one and burned-grazed by four, six and two plots, for a total of 32 plots.

Analysis. Plant patterns on each site were analyzed using Ripley's *K*-function (Ripley 1976; reviewed in Haase 1995) on the centers of occupied quadrats within the grids (as demonstrated in Fehmi and Bartolome 2001). Ripley's (1976) *K*-function (*L(t)*) was selected as a robust (Cressie 1991), powerful, and commercially available (Venables & Ripley 1999) method of testing for spatial patterns. Ripley's *K*-function has been defined as:

$$\hat{K}(t) = \frac{1}{\hat{\lambda}} \frac{1}{N} \sum_{j=1}^{N} \sum_{j \neq i} k_{ij} \qquad (1)$$

(Goreaud and Pelissier 1999) where $k_{ij} = 1$ when distances between points i and $j \leq t$ and $k_{ij} = 0$ when distances between points i and $j > t$. Intensity, $\hat{\lambda}$:

$$\hat{\lambda} = \frac{N}{S} \qquad (2)$$

is calculated with the number of points per unit area N, in size S. The variance of the process is stabilized with the statistic displayed as:

$$L(t) = \sqrt{K(t)/\pi} \qquad (3)$$

Advantages of the *K*-function include that it is easily interpreted, it has been often used in ecology (such as Haase 1995; Martens et al. 1997; Podani and Czárán 1997; Goreaud and Pelissier 1999; Fehmi and Bartolome 2002) and it may allow compar-
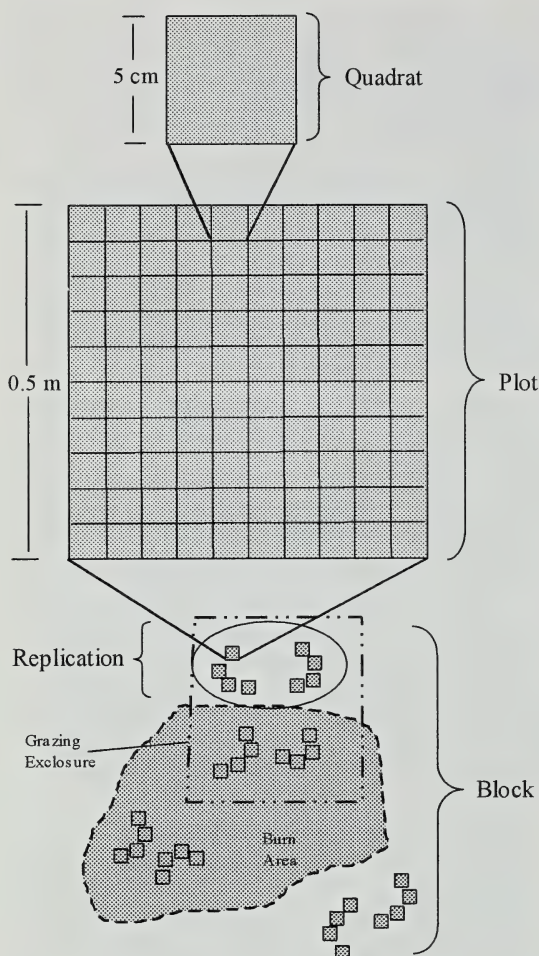
FIG. 1. Schematic diagram of sampling levels (not to scale). The experiment contained blocks (~0.25 ha), replications (~65 m²), plots (0.25 m²), and quadrats (25 cm²).

FIG. 2. An example plot showing the distribution of occupied quadrats (a) and the corresponding graph of the K-function (b). The dashed lines represents a 95% confidence interval based on 1000 Monte Carlo simulations. The graph (b) shows significant clumping on the plot up to 15 cm. This value was this plots contribution to the ANOVA for the experiment as a whole.

ison of both point-based and grid-based data (Fehmi and Bartolome 2001).

Confidence intervals (95%; CI) were calculated based upon 1000 Monte Carlo simulations of data on the grid (Cressie 1991). The CI was recalculated for each unique number of filled quadrats to reflect the corresponding change in confidence bounds and the upper and lower CI's were determined from the 97.5th and 2.5th quartiles of the simulated data. The standard edge correction of Ripley (1976) was used (*see* Goreaud and Pelissier 1999 for a review of edge corrections) to adjust the statistic to correctly estimate patterns as they continue outside the observed area. Plots with less than 10 occupied quadrats were not used for the analysis because they contain limited spatial pattern information. Plots with less than 15 occupied quadrats could only be used if at least half the data was near the

center of the plot due to loss of spatial information inherent to the plot edges and our edge correction.

The analysis gave estimates of spatial pattern at 12 scales (5–25 cm). A single value per plot was needed to analyze the data. Preliminary evaluation of the data revealed that 30 out of 32 plots had significant small-scale clumping and two were not clumped—with a clump being defined as a group of occupied quadrats. We then used the longest significant distance to represent the clump size and the two plots without observed clumping were assigned a distance of 5 cm (just below our minimum detection level, *see* Fig. 2). The 32 clump sizes (as determined by the K-function analyses) were analyzed using ANOVA in a nested model. The full model, with all main effects and interactions was tested, and insignificant terms were pooled into error. Assumptions of homoscedasticity were met, and transformations were not required to achieve normality of the data. The number of occupied plots and the total frequency of occupied quadrats per treatments were analyzed together in a Multivariate Analysis of Variance (MANOVA) to test for site level spatial patterns (*N. pulchra* distributions) associated with the treatments. A Pillai-Bartlett trace was used to generate F statistics (Insightful Corporation 2001).
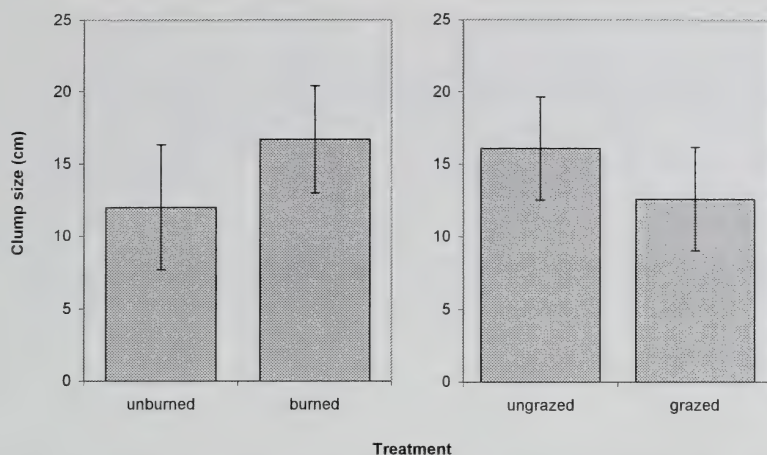
FIG. 3. Treatment effects on *Nassella pulchra* clump size. Clumps (groups of occupied quadrats) were significantly larger on burned sites than unburned (P = 0.03) and smaller on grazed sites than ungrazed sites (P = 0.05). Error bars represent 95% confidence intervals of the means. There were no interaction effects so treatment means are directly interpretable.

RESULTS AND DISCUSSION

The results show that burning and grazing have distinct but opposite effects on *N. pulchra* clump size (Fig. 3) at scales relevant to individual plants. The burning treatment significantly increased the clump size from 12.0 to 16.7 cm (F(1, 8) = 7.32, P = 0.03; Fig. 3) and the grazing treatment decreased the clump size from 16.1 to 12.6 cm (F(1, 8) = 5.06, P = 0.05; Fig. 3). There was no significant interaction between burning and grazing (P = 0.49) or reduction in variance from the blocks (P = 0.31). The lack of interaction effects allows direct interpretation of treatment means. Burning increased the clump size while grazing seemed to decrease it.

The buildup of plant litter is known to impede the growth of *N. pulchra* (Dyer et al. 1996) and both the grazing and burning evaluated here involved reduction in litter from moderate to severe (about 43% and 90% reduction in peak standing crop, respectively). However, because the effect of burning is associated with increased clumping and grazing with decreased clumping, the effect of litter is either not driving the spatial pattern or the size of the effect was swamped by other factors. Depending on timing and intensity, burning can decrease the populations of adjacent exotic annual grasses (Hopkinson et al. 1999), and annual grasses are known to compete with *N. pulchra* (Dyer and Rice 1999), as well as releasing scarce nutrients that may be available to perennials before new annuals have germinated.

Increased clumping of *N. pulchra* in the ungrazed plots may represent a strategic optimum for competition with neighboring plants (Adler et al. 2001) or the expression of abiotic factors altered by grazing (Fuhlendorf and Smeins 1999). Especially on ungrazed sites (Fehmi and Bartolome 2002),

California voles (*Microtus californicus*) can destroy substantial amounts of vegetation through construction of aboveground runways (Ford and Pitelka 1984). This seems to favor the larger clumps of *N. pulchra* because these runways go around larger clumps. An analysis of the genetics of clumps may give insight into the *N. pulchra* small-scale distribution, i.e., if they arise from a single plant or from a number of individuals (e.g., Lord 1993).

The changes in both clump size and distribution should reflect both the plant's mechanics of garnering resources and optimal demographic strategy in concert with the characteristics of disturbance. The small-scale patterns of grazing on the sites are unknown but likely to be important. Adler et al. (2001) point out that grazing could cause spatial patterns in the plants if the animals graze in a non-random pattern. No data on the spatial heterogeneity of grazing patterns was collected during our experiment. We assume our grazing was selective (non-random) because sheep primarily grazed our research areas, the stocking rate was low, and they grazed the site year-round. Sheep are known to graze selectively, grazing specific plants and plant parts (Heady and Torell 1959). The selectivity of their grazing would have been increased by the low stocking rate. This selectively should have impacted the perennial grasses because they are preferred forage (Heady et al. 1963) and green during the dry summer months when the annuals (roughly 40% of the foliar cover) were senescent. Our small-scale results support the hypothesis of Adler et al. (2001), based on a review of the available literature, that selective grazing increases heterogeneity. It is encouraging that a similar process can be inferred, with grazing changing the fundamental consequences of plant distribution across many types of grasslands.
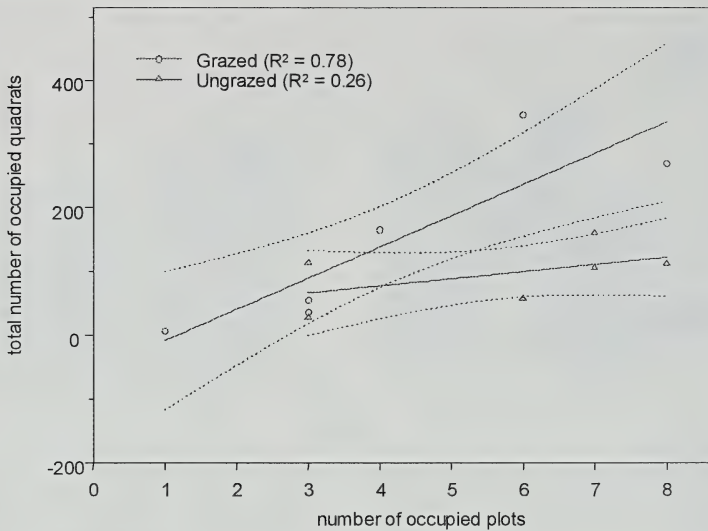
FIG. 4. The effects of the grazing (P = 0.08) treatment in the total number of quadrats occupied by *Nassella pulchra* and the number of occupied plots per replicate. There were 8 plots per replicate and 100 quadrats per plot. The dashed lines represents a 90% confidence interval for the solid regression lines.

Decreased clumping of *N. pulchra* in the grazed plots could have several causes. The resources available to the more widely distributed parts of the plant should be greater than those afforded by the more compact plants (Benjamin 1996). This palatable plant also benefits from being a more diffuse target for grazing, potentially reducing the ability of grazers to preferentially select them over their neighbors of other species. Distributing these plant parts also decreases the chance of plant mortality because each part is capable of independent existence (Briske and Hendrickson 1998). Unfortunately in this case, it is unclear whether disturbance is benefiting grasses, perhaps through the removal of litter and neighbors (Maschinski and Whitham 1989; Edwards 1995), or if the grasses are being negatively affected by being eaten or trampled (Maschinski and Whitham 1989; Huntsinger et al. 1996).

The effect of grazing may be scale specific because grazing seems to have some aggregation effect on the distribution of the *N. pulchra* clumps. Analysis of the site level analysis (the MANOVA) data (Fig. 4), showed that there were more occupied quadrats on fewer plots in the grazed treatment (F(2, 5) = 4.30, P = 0.08) which we interpret as site level increased heterogeneous distribution on the scale of the treated areas. The burning treatment analysis at this scale shows no effects (F(2, 5) = 0.22, P = 0.81) and there was no significant interaction between burning and grazing (P = 0.78) or reduction in variance from the blocks (P = 0.36). This analysis reflects the increased heterogeneous distribution of *N. pulchra* on the 65 m² treated areas of the park. We speculate that this change in distribution was due to plant-soil relationships where

mortality from grazing was dependent on soil resources and these soil resources were distributed heterogeneously. This type of relationship is not uncommon and Adler et al. (2001) review numerous examples where grazing changed plant distributions so that they corresponded to soil water and nutrient distributions. Perhaps the reduction of ~30% root growth as described for the tallgrass prairie (Johnson and Matchett 2001) also occurs in *N. pulchra* and could explain the reduction in distribution associated with grazing.

Larger plants more evenly distributed across the landscape, as suggested by the data from our burning treatment, seem likely to change the runoff and erosion potential. Perennial bunchgrasses, when present, translocate more of their net energy into roots (50% vs. 39% for annuals) and the translocation is evenly distributed through the growing season rather than primarily in early spring for annuals (Heady et al. 1991). Runoff events resulting in erosion typically occur in the early fall when annual grasses have not yet grown appreciably. Because underground decomposition rates for annuals are approximately double those for perennials in this system (1.2–5.4 mg g^{-1} d^{-1} vs. 0.8–2.4 mg g^{-1} d^{-1}), sites dominated by annuals could have higher erosion risk. If the 25% increase in root growth associated with burning in the tallgrass prairie (Johnson and Matchett 2001) were to also occur in *N. pulchra,* it would likely increase the resistance to erosion. Increases in *N. pulchra* would also increase the carbon storage of this system because it can deplete soil moisture to at least 150 cm while annuals tend to deplete only the top 30 cm (Dyer and Rice 1999).

Conclusions

If grazing and burning are to be effective management tools, we must understand not only the effects averaged across sites but also the impacts of these disturbances on plant distributions. Our results on plant distributions support the recommendation of earlier work by Hatch et al. (1991) that *N. pulchra* responds well to burning and grazing exclusion. This would be our recommendation for conservation, restoration, or enhancement of this species when sites have heavy levels of residual dry matter. However, the mix of native and introduced species on the site are quite likely to each have unique responses to burning and grazing (e.g., Hatch et al. 1999) and simple management formulas such as burning every fourth year are unlikely to satisfy common restoration goals. A mix of use (e.g., grazing and foot traffic), management (e.g., burning and exclosures) and frequent assessment has the potential to enhance both *N. pulchra* and site diversity. Determining the spatial pattern of species within the plant community structure is an important, but underutilized technique and the development of better methods for analysis and comparison will aid our understanding of these systems.

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PHENETIC AND INTERVARIETAL CROSSING DATA SUPPORT THE RECOGNITION OF *IRIS TENAX* VAR. *GORMANII* (IRIDACEAE), A RARE NORTHWEST ENDEMIC

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ABSTRACT

The taxonomic status of the western Oregon taxon, *Iris tenax* var. *gormanii* (Piper) Foster (Iridaceae), has been in dispute since soon after its description in 1927. It has been considered a distinct species, a variety of *I. tenax* Wats. and since the 1950's a color form of *I. tenax*. The status of the taxon was confounded by the extirpation of the only known population in the 1970's. During this study, fieldwork verified a remnant population of *I. t.* var. *gormanii* near the original site. A comparative, morphological phenetic study was undertaken of individuals at this site and three *I. t.* var. *tenax* sites. Interfertility of the two varieties was tested with in situ intervarietal hand pollination. Morphological data confirmed that *I. tenax* var. *gormanii* is distinct from *I. t.* var. *tenax*. Intervarietal crossing data found that interfertility between *I. t.* var. *tenax* and *I. t.* var. *gormanii* is lower than intrafertility indicating that partial reproductive barriers are present. Reproductive barriers are especially strong when *I. t.* var. *gormanii* functions as the female indicating that gene flow would be more likely from *I. t.* var. *gormanii* into the gene pool of *I. t.* var. *tenax* than in the reverse direction.

Key Words: Iridaceae, *Iris tenax*, intervarietal reproductive barriers, rare plants, species boundaries.

Iris tenax Wats. is a geophyte with deciduous, herbaceous, aerial shoots and perennial rhizomes. Inflorescences of *I. tenax* typically consist of a single flower. Occasionally, a second flower is borne on a pedicel below the terminal flower and opens after the terminal flower closes. Plants display several characteristics attributed to outcrossing taxa such as showy open flowers, nectar rewards, nectar guides, and many ovules per gynoecium. Considerable clonal reproduction occurs and older clumps of *I. tenax* can exceed 25 cm in diameter. The species occurs in western Washington and Oregon where it is found in light shade along roadcuts, in conifer forest openings, or in open, oak grasslands. The elevational range of *Iris tenax* is from about 10 m along the coast to about 2000 m on the western slopes of the Cascades. The species is typically lavender to purple-flowered, although white and gray forms are found. *Iris tenax* is one of about 18 taxa within *Iris* series *Californicae*, a series that is restricted to the Pacific Coast region.

Piper (1924) described a yellow-flowered *Iris* from the banks of Scoggins Creek in Washington County, Oregon. He considered this *Iris* a new species and named it after M. W. Gorman, the original collector. Foster (1937) reduced the taxon to *I. t.* var. *gormanii* (Piper) R. C. Foster. Lenz in his 1958 monograph of *Iris* series *Californicae* did not recognize *I. t.* var. *gormanii* because he considered the taxon within the typical morphological variability of *I. tenax*. Lenz considered flower color an insufficient character for the determination of taxa within *Iris* series *Californicae*.

Piper reported that sexual reproduction was low for the newly discovered yellow *Iris* and estimated capsule production at 5%. Such low fertility could be an indication that the taxon is of hybrid origin. A hybrid origin has been postulated for other *Iris* series *Californicae* taxa (Lenz 1958, 1959; Clarkson 1959, 1962). Populations of plants with intermediate morphology have also been identified and proposed as sites of hybridization between *Iris* series *Californicae* species (Lenz 1959; Clarkson and Thompson 1961; Carter and Brehm 1969). The yellow-flowered *Iris* at Scoggins Creek, however, was not considered a hybrid because its morphology was not similar to other yellow-flowered *Iris* (Clarkson 1959). Although Clarkson did not elaborate, the shorter floral tube and wider flowers of *I. t.* var. *gormanii* distinguish it from other yellow-flowered Iris. In addition, only one other taxon, *I. t.* var. *tenax*, occurs in the area.

Interest in this yellow-flowered *Iris* increased in the late 1970's when botanists searched herbarium records and field locations for plants that might be candidates for protection under the Endangered Species Act. It was determined that the original and only known location for the yellow *Iris* was covered by water in 1975 when the Hagg Lake Reservoir, a recreation site in the Coast Range foothills, filled after Scoggins Creek was dammed. Additional populations were not located during fieldwork at the reservoir in the 1970's and 1980's. Cream colored flowers were reported at a site in the coast range (Clarkson 1959) leading to some confusion about the flower color of the original population.

Studies by Smith and Clarkson (1956) and Lenz (1959) demonstrated that members of *Iris* series *Californicae* can be crossed with fertile offspring produced from all combinations attempted. No quantification of the relative success of interspecific crosses was reported. Their crossing studies did not include the Scoggins Creek *Iris*.

The current study examined the taxonomic status of the Scoggins Creek *Iris* by addressing three specific questions. The first was to determine if there are existing populations. The second was to determine if this yellow-flowered *Iris* is a distinct taxon. Finally, fertility between the yellow-flowered Scoggins Creek *Iris* and the purple-flowered *I. tenax* was tested to determine if reproductive barriers exist.

MATERIALS AND METHODS

Study sites. The area around Hagg Lake was searched each spring for three consecutive years from 1990 to 1992 for a yellow-flowered *Iris*. In the first two years, fieldwork was conducted in April and early May while in year three fieldwork was conducted in May and June. The herbaria at Oregon State University (OSH) and Portland State University (HPSU) were surveyed for additional locations of *I. tenax* with yellow or cream flowers. Four sites were located: outside of Scio, near Mc-Minnville, Monument Peak, and Multnomah Falls. Populations near these sites were then field surveyed for yellow-flowered *Iris*.

All final fieldwork was carried out at five other sites: one in southwestern Washington and four in western Oregon. Purple *I. tenax* occurred at four of these sites, 90 km north of the Washington-Oregon border near the town of Toledo, Portland's Hoyt Arboretum, 40 km east of Portland near the town of Corbett, and 80 km south of Eugene in Rice Valley. The fifth site, 30 km southwest of Portland along Scoggins Creek, was the only known site for the yellow-flowered *I. tenax* (hereafter referred to as var. *gormanii*). This population is subdivided into an upper, relatively flat area and a sloping area along a road cut. Voucher specimens are deposited at the Jepson Herbarium (JEPS) (collection numbers, 92-ph-6, 93-re-23, 92-ph-28, 92-ph-5 and 92-ph-29, respectively).

Phenetic studies. Four of the five populations, Toledo, Corbett, Rice Valley, and Scoggins Creek were used in phenetic studies. Populations of *I. t.* var. *tenax* were chosen to represent the geographical range of the variety. The Toledo population represents a northern population while Rice Valley represents a southern population. The Corbett population is central within the *I. t.* var. *tenax* range and is within 80 km of the Scoggins Creek population of *I. t.* var. *gormanii*. Fieldwork was conducted in 1992, 1997 and 2001. Data on 13 characters were taken from 10 individuals at each of the four populations. Data included counts (number of leaves), qualitative data (flower color), and mea-

surements (length of filament, anther, and pedicel; and length and width for bracts, sepals, petals, and style lobes). Flower color was coded as purple or yellow. The data set was standardized (Z-scores computed) prior to principle component analysis (PCA), using SPSS 10.0 (SPSS Inc., Chicago, IL) and the Pearson correlation method of determining distances between variables.

Pollination studies. Three of the five populations were used for pollination studies, Hoyt Arboretum, Corbett, and Scoggins Creek. Populations were chosen based on elevational differences that extended the bloom time of *I. t.* var. *tenax*. Fieldwork was conducted in 1993 and 1994 and consisted of male gamete viability tests and crossing experiments. When possible, pollen was transferred between sites in the morning of the same day.

Fresh and two-day old pollen was tested for viability using an alcohol dehydrogenase test (Dafni 1992, protocol 5). Five flowers representing five individual genets were collected for analysis at each site. Immediately upon return to the laboratory fresh pollen viability was determined using approximately 200 pollen grains from one anther of each of the five flowers. Viability of 2-day old pollen was determined by analyzing 200 pollen grains from a second anther of each flower after refrigeration at 4°C for 24–30 hr. Time of receptivity of stigmas was also determined based on a test for alcohol dehydrogenase (Dafni 1992, protocol 5).

For field pollination studies two treatments were used: xenogamous outcrossing and intervarietal crossing. Ninety-nine plants used as female receptors in outcrossing treatments were prepared by removal of ripe anthers from terminal flowers that were not yet in female phase and placement of gelatin tubes (½ of a gelatin capsule) over each of the three style crests to exclude pollinators. The following day pollen was removed from anthers of five to ten individuals of a population using toothpicks, mixed, and placed on receptive stigmas of different plants of the same population. Gelatin tubes were replaced over the pollinated stigmas. The pollen mixture should have minimized any interactions between specific pollen donors and female plants.

The same procedure used for outcrossed plants was used in intervarietal crosses except that pooled pollen was stored in empty gelatin capsules and applied to stigmas of the opposing variety the same day. Occasionally pollen was stored at 4°C and applied the following day. Pollen was available in all three populations for 127 reciprocal crosses. The flowering time of *I. t.* var. *gormanii* overlapped with the two *I. t.* var. *tenax* populations although overlap was greatest with the higher elevation Corbett population. Because of differences in flowering times, pooled pollen of *I. t.* var. *tenax* used in intervarietal crosses varied in composition. Early in the season pooled pollen was only from plants at the Portland population, in midseason pooled pol-
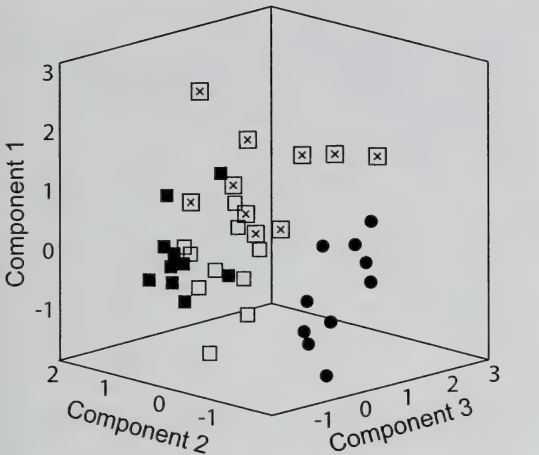
Corbett □   Rice Valley ⊠   Toledo ■   Scoggins Creek ●

FIG. 1.   Principal components analysis of *Iris tenax* var. *tenax* (Corbett, Toledo and Rice Valley populations) and *I. t.* var. *gormanii* (Scoggins Creek population) based on 13 morphological characters.

TABLE 1.   CHARACTER VALUE MEANS ± SE FOR *I. T. VAR. TENAX* and *I. T. VAR. GORMANII.* Measurements are in cm.

Characters	*gormanii*	*tenax*
Flowers: purple (0), yellow (1)	1.00 ± 0.00	0.00 ± 0.00
# cauline leaves	2.00 ± 0.00	2.80 ± 0.10
Floral bract length	5.97 ± 0.21	5.81 ± 0.13
Floral bract width	0.78 ± 0.04	0.81 ± 0.02
Sepal length	5.58 ± 0.12	5.97 ± 0.11
Sepal width	3.36 ± 0.95	2.47 ± 0.04
Petal length	4.87 ± 0.15	5.31 ± 0.10
Petal width	1.29 ± 0.07	1.43 ± 0.03
Style crest length	3.59 ± 0.08	3.81 ± 0.08
Style crest width	1.20 ± 0.05	1.16 ± 0.04
Pedicel length	2.07 ± 0.15	2.70 ± 0.27
Filament length	0.70 ± 0.00	0.90 ± 0.10
Anther length	1.32 ± 0.04	1.50 ± 0.04

len was from both populations and late in the study pooled pollen was only from the Corbett population.

Pollen tube growth within styles of *I. t.* var. *gormanii* and *I. t.* var. *tenax* was analyzed after each of the two pollination treatments. Whole styles were collected from 14 plants at 12, 24 and 72 hrs post-treatment and preserved in 70% alcohol. Prior to study, styles were rinsed in distilled water, placed on a slide, stained with either 0.1% aniline blue (Dafni 1992, protocol 18) or 0.005% aniline blue (Jensen 1962) and observed using fluorescence microscopy.

Two hundred and sixteen fruits resulting from each of the pollination treatments were collected prior to the completion of fruit maturation at 13 to 17 d after pollination. Development of fruits and seeds may be overestimated in this study because they were analyzed prior to final maturation. This time interval was chosen because expanded ovules and ovaries were easily identified and insect damage was minimal. Collected fruits were identified as developed (enlarged and light green) or not developed (small and yellow-green to brown). Ovules within each of the three locules of developing fruits were identified as either developed or not developed. Ovules were considered developed only if they showed significant enlargement and did not display signs of deterioration such as turning yellow or collapsing. Ovaries with insect damage were not included in the analysis. Parametric Analysis of Variance (ANOVA) statistics were performed to determine if taxon or treatment effects were significant.

RESULTS

Search for I. t. *var.* gormanii. Populations of *Iris* at the four additional sites identified from herbarium specimens (Scio, McMinnville, Monument Peak, and Multnomah Falls) were comprised of mostly lavender to purple-flowered plants with a few white, cream, and/or gray flowers present. No yellow flowers were found in these populations. A population of yellow-flowered *Iris* was found approximately two km north of Hagg Lake Reservoir during the third year. Fieldwork in the third year was conducted later than *I. t.* var. *tenax* is typically in bloom. Peak bloom time for *I. t.* var. *tenax* at low elevations is mid-April to mid-May whereas the yellow-flowered population at Hagg Lake Reservoir did not begin bloom until late-May. This population is estimated at about 1000 plants along a road cut and in an adjacent logged area. The logged area was replanted to Douglas fir in the 1980's. Most of the area surrounding the reservoir is oak grassland. Typical purple-flowered *I. t.* var. *tenax* was found in two areas on the road cut circling the reservoir but no purple flowers were closer than two kilometers to the yellow-flowered population. In late May fruits rather than flowers were present on purple-flowered *Iris* at the reservoir. The Monument Peak population was revisited in early June and all flowers were in fruit.

Phenetic studies. Individuals from Scoggins Creek, the only known population of *I. t.* var. *gormanii* grouped together (Fig. 1). The three populations of *I. t.* var. *tenax* did not form distinct groups but instead formed one large group (Fig. 1). Five Rice Valley and two Corbett individuals did not fall within the cohesive main grouping but were instead spread out within the space defined by the three components. The first three components represented 61% of the variability present in the data set. The mean and standard error of each of the 13 characters for the two taxa are given in Table 1. Table 2 gives the loadings of characters on the three

TABLE 2. LOADINGS OF CHARACTERS ON THE FIRST THREE PRINCIPAL COMPONENTS.

Characters	Components		
	1	2	3
Flower color	−0.446	−0.502	0.535
# cauline leaves	0.184	0.788	−0.272
Floral bract length	0.336	−0.274	0.203
Floral bract width	0.482	−0.008	0.128
Sepal length	0.890	−0.007	0.152
Sepal width	0.438	0.624	0.371
Petal length	0.832	0.006	0.101
Petal width	0.459	0.550	0.491
Style crest length	0.793	−0.310	−0.009
Style crest width	0.490	−0.289	0.429
Pedicel length	0.766	−0.321	−0.274
Filament length	0.671	−0.219	−0.391
Anther length	0.324	0.007	−0.355

FIG. 2. A. Style with style crest and stigmatic flap (sf). Stamen occurs opposite style. B. Male phase of flowering, stigmatic flap is appressed to style crest. C. Female phase of flowering, stigmatic flap is recurved. Scale bars = 1 cm.

components, indicating the relative importance of each character in defining the two clusters. Each component contributed to the separation of the two taxa, indicating that each character was important in this study. Loadings along component 1 were moderate to high for all characters; however, this component did not separate most of the individuals representing these taxa. This is because the two taxa are similar in overall size, although *I. t.* var. *tenax* is somewhat larger for eight of the 11 measured characters. Greatest separation occurred along component 2, reflecting critical differences between these two taxa in flower color, number of cauline leaves, sepal width, and petal width.

Pollination studies. Pollen viability is high for both varieties. Viability of fresh pollen averaged 92% for *I. t.* var. *tenax* and 93% for *I. t.* var. *gormanii.* Two-day old pollen viability averaged 90% for *I. t.* var. *tenax* and 95% for *I. t.* var. *gormanii.* The stigmatic flap is borne abaxially on a petaloid style (Fig. 2a) and is appressed to the style during

the male phase of flowering (Fig. 2b). Stigmas of both taxa were receptive at the morphological female phase when the stigmatic flap is recurved (Fig. 2c).

Figure 3a shows a typical ovary of *I. tenax* var. *gormanii.* Part of the ovary wall has been removed exposing one of the three locules. Six ovules are developing normally, one ovule began to enlarge but is now degenerating (at arrow) and several ovules show little or no development. The percent of *I. t.* var. *tenax* ovules with normal development at 17–20 days after outcross pollination is similar for both years (Table 3). Results for *I. t.* var. *gormanii* are also similar for both years. In general, however, survival of ovules is lower for *I. t.* var. *gormanii* than for *I. t.* var. *tenax* (Table 3). Ovule survival is slightly lower for both taxa when intervarietal crosses are made with the exception of crosses made in 1994 with *I. t.* var. *tenax* as the female. Differences in ovule survival between the two taxa are significant (P < 0.01). Differences ob-

FIG. 3. Pollination and development of ovules and fruits of *Iris tenax.* A. Fruit with developing and non-developing ovules; ovule at arrow began development but then failed, ×2.5. B. Non-developed and developed fruits, ×1.5. C. Pollen tubes in style, (×150).

TABLE 3. PERCENTAGE OF OVULES AND OVARIES WITH NORMAL DEVELOPMENT. Data are means ± SE. Flowers of *Iris tenax* var. *tenax* and *I. tenax* var. *gormanii* were subjected to two pollination treatments over two field seasons. N = number of plants. Significance at P < 0.02 was found between years combined across all treatments and both taxa; P > 0.05 between treatments and taxa.

Female parent	Outcross-pollinated (%)				Intervarietal cross (%)			
	N	Ovules	N	Ovaries	N	Ovules	N	Ovaries
var. *tenax* 93	14	38.8 ± 5.3	26	65.6 ± 11.1	14	30.4 ± 5.4	35	45.0 ± 14.1
var. *tenax* 94	16	30.6 ± 4.0	22	64.3 ± 11.8	15	33.7 ± 3.8	23	68.1 ± 12.0
var. *tenax* 93–94	30	34.4 ± 3.3	48	64.9 ± 3.3	29	32.1 ± 3.3	58	50.4 ± 13.1
var. *gormanii* 93	04	34.9 ± 11.3	17	48.5 ± 5.0	02	18.0 ± 1.2	29	06.1 ± 03.1
var. *gormanii* 94	22	31.2 ± 3.3	23	63.0 ± 6.9	12	21.1 ± 6.2	32	45.8 ± 16.9
var. *gormanii* 93–94	26	31.7 ± 3.3	40	55.8 ± 5.5	14	20.6 ± 3.6	61	21.9 ± 11.1

served in ovule survival between treatments are not significant (P > 0.05).

Figure 3b illustrates a normally developing and a failing ovary of *I. t.* var. *gormanii*. Results from this study show two patterns in ovary development across the two treatments (Table 3). First is the lower percent of *I. t.* var. *gormanii* ovaries that survived to 17–20 days after pollination when compared to ovary survival in *I. t.* var. *tenax*. Second, intervarietal crosses resulted in lower ovary survival for both varieties in 1993 and for *I. t.* var. *gormanii* again in 1994. Differences between taxa for ovary survival are significant (P < 0.001). Differences between the two pollination treatments were not detectable with the statistical tests used (P > 0.05).

Overall reproductive success of intervarietal crosses was 4% when *I. t.* var. *gormanii* was female and 16% when *I. t.* var. *tenax* was female (Table 4). This is compared with 18% for *I. t.* var. *gormanii* and 22% for *I. t.* var. *tenax* with xenogamous outcrossing (Table 4).

Pollen tube growth was similar following both treatments. Germinated and ungerminated pollen could be seen on stigma surfaces 12 hrs after pollination. By 24 hr after pollination pollen tubes were observed within styles and ovaries (Fig. 3c). Some pollen tubes could be seen entering ovules.

DISCUSSION

Although it is possible that additional populations of *I. t.* var. *gormanii* are present near the original site or at other sites not investigated, it is clear that this taxon is rare. Only the single population near the historical collection site was found. Three years of fieldwork around Scoggins Creek and at other sites in the Coast Range did not result in the location of additional populations. The population of *I. t.* var. *gormanii* at Scoggins Creek displayed very little color variation. Most flowers were butter-yellow although a few were pale-yellow. Sites in the Coast Range reported to have cream-colored *Iris* represented *I. t.* var. *tenax* populations that were comprised of mostly lavender to purple plants but had some cream, white or gray-flowered forms. Small bees and flies were observed pollinating *I. t.* var. *gormanii* flowers, while bumblebees were frequent pollinators of *I. t.* var. *tenax* flowers (Wilson 2001).

Morphological data support the recognition of two taxa. Phenetic analyses resulted in separation of *I. t.* var. *gormanii* from var. *tenax*. Although there are differences, these two taxa are quite similar in morphology, supporting Fosters retention of Piper's *I. gormanii* within *I. tenax* as a variety. Status as a variety is also in agreement with molecular sequence data that indicates a recent divergence between these two taxa (Wilson 2003). In general, *I. t.* var. *gormanii* is smaller than *I. t.* var. *tenax* and this is reflected in floral and vegetative organ measurement means. Other than size, distinctive characters include flower color, number of cauline leaves, and floral bract and style crest shape. Bracts of *I. t.* var. *gormanii* are longer and narrower than bracts of *I. t.* var. *tenax* while style crests of *I. t.* var. *gormanii* are wider and shorter. Sepals of *I. t.* var. *gormanii* are also wider than sepals of *I. t.* var. *tenax* while petals are shorter.

Partial reproductive barriers occur between *I. t.* var. *tenax* and *I. t.* var. *gormanii*. Overall estimated reproductive success of intervarietal crosses was 4% when *I. t.* var. *gormanii* was female and 16%

TABLE 4. ESTIMATED REPRODUCTIVE SUCCESS BASED ON POTENTIAL SEED DEVELOPMENT. Values are the product of the mean percent of ovules and ovaries (ovules × ovaries) with normal development (see Table 3).

Female parent	Outcross-pollinated (%)			Intervarietal cross (%)		
	1993	1994	1993–1994	1993	1994	1993–1994
var. *tenax*	25.4	19.6	22.3	13.7	22.9	16.2
var. *gormanii*	16.9	19.6	17.7	1.1	9.7	4.5

when *I. t.* var. *tenax* was female. When compared to xenogamous outcrossing, these results indicate a 27% loss of fertility for intervarietal crosses when *I. t.* var. *tenax* is female and 78% loss when *I. t.* var. *gormanii* is female. These findings are not associated with a general lack of fertility for *I. tenax* because the results of xenogamous outcrossing are similar to other *Iris* species (Planisek 1983; Kron, Stewart and Back 1993; Wilson 2001) and plants in general (Wiens 1984; Sutherland 1986). Some of these studies analyzed only ovaries (Planisek 1983; Sutherland 1986) or ovules (Wiens 1984).

Reproductive barriers are especially strong when *I. t.* var. *gormanii* functions as the female. This indicates that gene flow would be more likely from *I. t.* var. *gormanii* into the gene pool of *I. t.* var. *tenax* than in the reverse direction. Studies on reproductive success of interspecific hybridizations between *I. fulva* and *I. hexagona* (Carney et al. 1994) show similar patterns where fruit set was significantly depressed with interspecific pollination when *I. fulva* acted as the female parent. Fruit development was normal when *I. hexagona* was the female in interspecific crosses. In my study ovary development was depressed in 1993 and the combined data set when *I. t.* var. *tenax* acted as female and *I. t.* var. *gormanii* as male. In reciprocal crosses ovary development was depressed in both years and particularly strongly in 1993. The pattern of unidirectional reproductive barriers is especially evident when ovary and ovule success are both considered.

It is possible that occasional intervarietal crosses occur between *I. t.* var. *gormanii* and *I. t.* var. *tenax* in nature. A few individuals of *I. t.* var. *tenax* occur within two kilometers of the only known population of *I. t.* var. *gormanii*. However, there is significant temporal separation between the two varieties that may limit their ability to cross. Flowering was completed for the *I. t.* var. *tenax* near Scoggins Creek prior to flowering of *I. t.* var. *gormanii*. The proposed varietal status for *I. t.* var. *gormanii* reflects the theory that speciation is recent and not complete between these two taxa. The reproductive barriers present would limit gene transfer from *I. t.* var. *tenax* to *I. t.* var. *gormanii* suggesting that this incipient species will continue its divergence.

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INFLUENCE OF ENVIRONMENTAL FACTORS ON THE REGENERATION OF HARDWOOD SPECIES ON THREE STREAMS IN THE SIERRA NEVADA

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Abstract

Regeneration of hardwood species on three streams in the northern Sierra Nevada was correlated with several environmental factors. The occurrence of seedlings of *Salix lutea* (yellow willow), *Salix laevigata* (red willow), and *Alnus tenuifolia* (mountain alder) were negatively correlated with canopy cover and litter depth, and positively correlated with solar radiation. All three species occurred more frequently on sandy soils where the stream channel was wide and the slope was relatively shallow. The occurrence of *Populus fremontii* (black cottonwood) seedlings was negatively correlated with canopy cover, and sandy soils, and positively correlated with distance from the watercourse and solar radiation. *Acer macrophyllum* (big leaf maple) and *Cornus sericea* (American dogwood) seedlings occurred under relatively dense canopy cover, in low light environments, but were limited to sandy soils and wide stream channels. Results indicate that the hardwood species that exist in riparian corridors within the Sierra Nevada mixed conifer forest type are variably reliant on conditions common to flood prone areas such as sandy mineral soils and a high light environment for regeneration.

Key Words: Hardwood regeneration, riparian, alder, willow, cottonwood.

Riparian woodlands cover a relatively small, but ecologically significant, portion of the landscape of the mid-elevation Sierra Nevada. Riparian communities are distinct from the forest matrix in which they exist in their structure, species composition, and provide habitat for a variety of terrestrial and aquatic wildlife species (Holstein 1984). An understanding of the processes that affect the recruitment riparian hardwood species is essential to the proper management of these systems.

The mixed conifer forest is dominated by a variety of coniferous species including *Abies concolor* (Gordon and Glend.) Lindley (white fir), *Pinus ponderosa* Laws. (ponderosa pine), *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir), and *Calocedrus decurrens* (Torrey) Florin (incense cedar). Hardwood species that coexist in this forest type, such as *Quercus kelloggii* Newb. (black oak) and *Quercus crysolepis* Liebm. (maul oak), tend to be highly adapted to xeric summer conditions. In contrast, the woodlands that grow along streams within the same elevation zone include drought intolerant species such as *Populus fremontii* S. Watson (black cottonwood), *Alnus tenuifolia* Nutt. (mountain alder), *Acer macrophyllum* Pursh (big-leaf maple), *Salix laevigata* Bebb. (red willow) *S. lutea* Nutt. (yellow willow), and *Cornus sericea* L. (dogwood)

(Russell and McBride 2001). The environmental factors that determine the range of each of these species are not clear, and the degree to which each is limited to the riparian zone is variable. *Salix* species, for example, are restricted to a narrow stream side band, while *C. sericea* grows along floodplains and on the lower portions of mountain slopes (Holstein 1984; McBride and Strahan 1984).

Species composition in the riparian zone is influenced by the processes of fire and flood (Andrus and Froelich 1988; Minore and Weatherly 1994). The ecological importance of fire is reduced in the riparian zone and is complicated by dynamic fluvial processes such as flooding and stream channel migration. In the absence of fire the dominance of coniferous species increases and hardwood dominance decreases (Russell and McBride 2001). In contrast, recurrent floods may encourage hardwood species (Glinski 1977; Lisle 1989; Trush et al. 1989). Hardwood regeneration is determined in part by the height of the water table (McBride and Strahan 1984) and may also be related to soil characteristics, and solar radiation (Shanfield 1984). The purpose of this study was to determine the variables important in the regeneration of hardwoods by addressing the following questions: 1. Is the density of hardwood seedlings of various species correlated

TABLE 1. RESULTS OF LOGISTIC REGRESSION ANALYSES OF REGENERATING HARDWOOD SPECIES WITH TWENTY-SIX INDEPENDENT VARIABLES MEASURED ON THREE STREAMS IN THE SIERRA NEVADA MIXED CONIFER FOREST.

	Coefficient	P-value
Acer macrophyllum R^2 = 0.640		
% cover	0.041	0.003
litter weight	0.815	<0.001
bank full width	0.054	0.001
slope	−0.053	0.003
elevation	−0.007	<0.001
Alnus tenuifolia R^2 = 0.584		
% cover	−0.035	<0.001
litter weight	−0.883	<0.001
bank full width	0.060	<0.001
height from creek	−0.422	0.005
relative frequency (loam)	−2.266	0.030
Cornus sericea R^2 = 0.357		
% cover	0.069	<0.001
% cover (conifer)	0.020	<0.014
litter weight	0.012	<0.001
litter depth	0.422	0.045
relative frequency (sand)	1.097	0.019
Populus fremontii R^2 = 0.426		
% cover	0.041	0.040
litter weight	0.095	<0.001
bank full width	0.016	0.016
distance to creek	−0.038	0.016
relative frequency (loam)	−1.185	0.006
Salix laevigata R^2 = 0.495		
% cover	−0.054	<0.001
% cover (hardwood)	−0.635	<0.001
litter depth	−0.322	0.012
distance to creek	−0.054	<0.001
relative frequency (sand)	0.936	0.047
Salix lutea R^2 = 0.471		
% cover	−0.038	0.026
litter weight	−0.565	0.007
litter depth	0.377	0.024
distance to nearest tree	0.014	0.004
aspect	0.019	<0.001

with biotic factors such as total canopy cover, the canopy cover of conifers, the canopy cover of hardwoods, and the distance to the closest tree? 2. Is the density of hardwood seedlings of various species correlated with soil parameters, such as, texture, litter depth, and litter weight? 3. Is the density of hardwood seedlings of various species correlated with factors related to location within the stream profile, such as, height from stream, distance from stream, bank full width, aspect, and elevation?

METHODS

A total of ninety 10-meter wide transects were randomly located perpendicular to three class-two streams and their tributaries within Lassen National Forest including thirty transects on each Deer Creek, Mill Creek, and the North Fork of the Feath-

er River. Data were collected within each transect from stream bank to the edge of the riparian zone. Additional randomly located transects that included no hardwood regeneration were designated as "no-regeneration samples" and were sampled for comparison. General information gathered for each transect included elevation, slope, aspect, bank full width, and stream height (sampled on three successive dates from a fixed point to estimate change in water level).

The following data were gathered within each transect at the location of each hardwood seedling less than 2 meters in height and at no-regeneration sample points: 1. Height and identity of each seedling, and a determination of the origin of each sample (i.e., seedling or root sprout). 2. Total percent canopy cover (measured with a spherical densiometer), percent conifer cover, and percent hardwood cover. 3. The percent solar radiation each month during the growing season, May through October, measured once at each transect using a solar pathfinder. 4. Litter depth and separate measures of hardwood and conifer litter weight. 5. Height and distance from the creek. 6. Soil texture, and volume of substrate particle sizes (<2 mm, 2–5 mm, 5–10 mm, 10–25 mm, >25 mm). Soil samples of equivalent volume were passed through a soil sieve. The volume of each particle size class measured through water displacement in a manner described in McBride and Strahan (1984).

The importance of the sample variables in explaining the occurrence of each hardwood regeneration sample was determined several statistical methods. Multiple logistic regression analysis was performed for each commonly occurring hardwood species with 26 independent variables. Analysis of variance (ANOVA) F-tests were used to compare the variation between each species and the no-regeneration samples in relation to individual ecological variables.

RESULTS

Six hardwood species were found in abundances high enough to facilitate statistical analysis including *Acer macrophyllum, Alnus tenuifolia, Cornus sericea, Populus fremontii, Salix laevigata,* and *S. lutea.* The variables with the greatest correlation with the occurrence of individual species, resulting from logistical regression analysis, were retained in each model. The environmental factors correlated with the presence of regeneration were species dependent. However, several factors were correlated with the presence of multiple species (Table 1).

Percent canopy cover was correlated with all six hardwood species included in the analysis. Four species including *A. tenuifolia* (F = −2.38, P = 0.023), *P. fremontii* (F = −5.37, P < 0.001), *S. laevigata* (F = −8.78, P < 0.001), and *S. lutea* (F = −6.98, P = 0.002), exhibited negative correlations with canopy cover, as well as average canopy
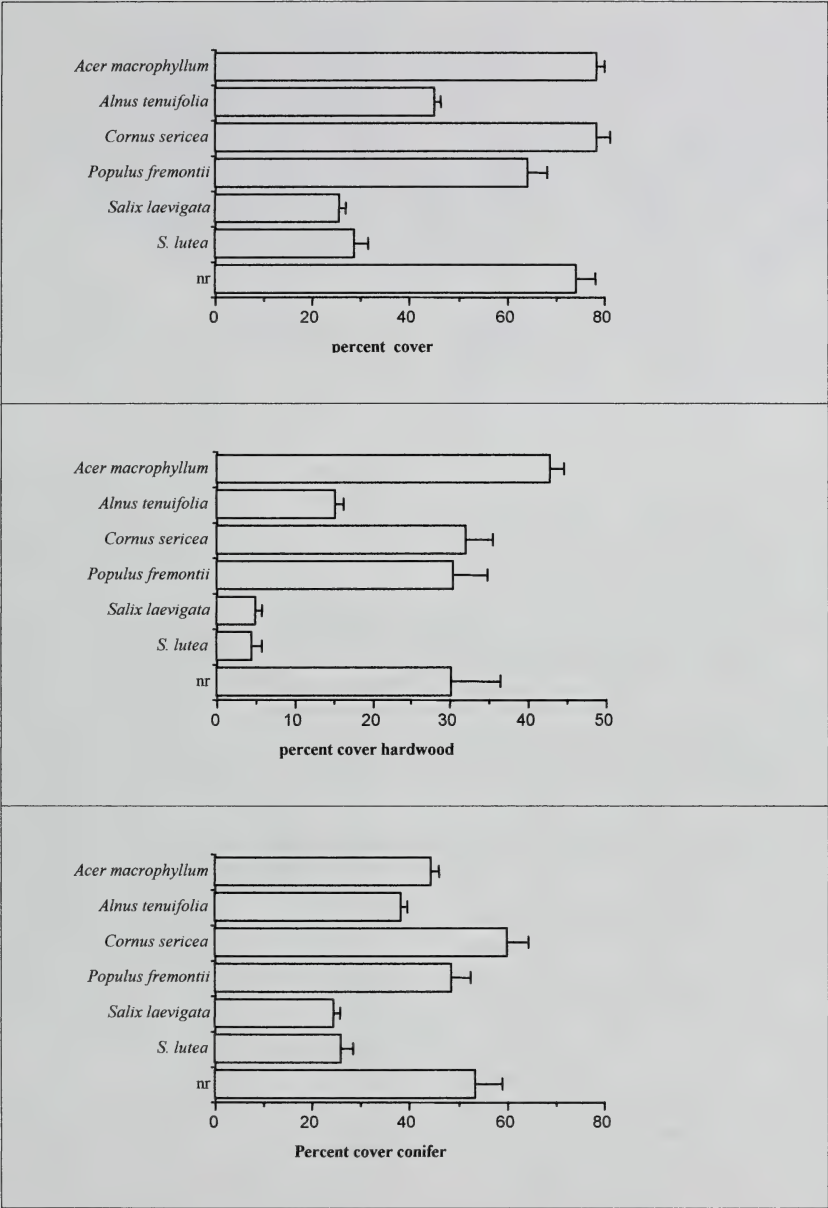
FIG. 1.   The average total percent canopy cover, percent canopy cover of hardwoods, and percent canopy cover of conifers, measured over hardwood seedlings on three streams in the Sierra Nevada mixed conifer forest. "nr" = no-regeneration samples. Error bars indicate standard error.

covers that were significantly lower than the no-regeneration samples (Fig. 1). Average canopy cover measured for the two *Salix* species was quite low. The canopy cover for *A. tenuifolia* and *P. fremontii* seedlings was somewhat higher but still significantly lower than the no-regeneration samples. *A. macrophyllum* and *C. sericea* seedlings had positive correlations to canopy cover but were not sig-

nificantly different from the no-regeneration samples (F = 1.23, P < 0.001; F = 22.34, P = 0.002).

Comparisons between each species with no-regeneration samples indicated that the percent hardwood cover (Fig. 1) and percent conifer cover (Fig. 1) measured over willow (F = −9.61, P = 0.034; F = −5.89, P = 0.008) and alder (F = −0.03, P < 0.001; F = −0.04, P < 0.001) seedlings were also

FIG. 2. The average percent solar radiation from May to October measured over hardwood seedlings on three streams in the Sierra Nevada mixed conifer forest. "nr" = no-regeneration samples. Error bars indicate standard error.

FIG. 4. Average bank full width (BFW) measured at random sample points on three streams in the Sierra Nevada mixed conifer forest. "nr" = no-regeneration samples. Error bars indicate standard error.

significantly lower than the no-regeneration samples. The percent cover of hardwoods and conifers for *A. macrophyllum, C. sericea* and *P. tenuifolia* seedlings was in the range of error of the no-regeneration samples.

Analysis of the percent solar radiation between May and October yielded similar results (Fig. 2). Both species of *Salix* (F = 122.08, P = 0.001; F = 98.95, P < 0.001), *A. tenuifolia* (F = 0.006, P = 0.001), and *P. fremontii* (F = 0.274, P = 0.003) seedlings all averaged significantly higher levels of solar radiation than the no-regeneration samples. In contr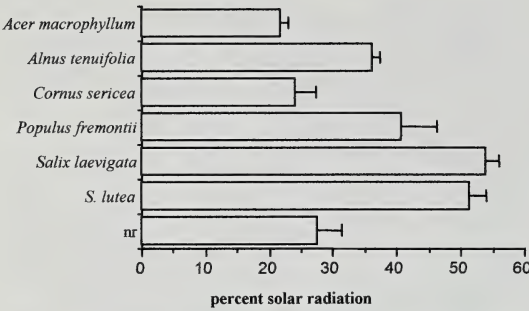ast, the average percent radiation measured for *C. sericea* and *A. macrophyllum* seedlings was within the statistical error range of the no-regeneration samples.

Litter weight was correlated with five out of the six species included in the analysis. Species with measures that averaged less than the no-regeneration samples included both *Salix* species (F = −2.210, P = 0.002; F = −1.507, P = 0.001) and *A. tenuifolia* (F = −0.127, P = 0.002) (Fig. 3). Species with measures that averaged greater than the no-regeneration samples included *A. macrophyllum* (F = 0.267, P = 0.001), *C. sericea* (F =

0.316, P = 0.001), and *P. fremontii* (F = 6.788, P < 0.001). No significant difference was found between the relationship of species to hardwood and conifer litter separately and their relationship to total litter weight. Analysis of litter depth yielded similar results.

Bank full width (BFW) had significant positive correlations with several species. Analysis indicates that all sampled species including *A. macrophyllum* (F = 0.51, P = 0.048), *A. tenuifolia* (F = 0.475, P = 0.035), *C. sericea* (F = 4.38, P = 0.002), *P. fremontii* (F = 6.25, P = 0.014), *S. laevigata* (F = 25.06, P = 0.003), and *S. lutea* (F = 14.27, P = 0.005), occurred more frequently on sites with stream channel widths significantly greater than the no-regeneration samples (Fig. 4). In a similar fashion, the average slopes on which hardwood seedlings tended to occur were generally less than the average slope of the no-regeneration samples for *A. macrophyllum* (F = −6.81, P = 0.001), *A. tenuifolia* (F = −46.02, P < 0.001), *P. fremontii* (F = −0918, P = 0.038), *S. laevigata* (F = −15.92, P < 0.001), and *S. lutea* (F = −2.78, P = 0.025) (Fig. 5).

Soil texture data indicate that sand, determined by analysis of particle size, was the most common
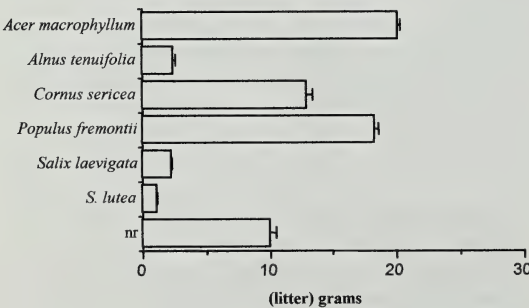

FIG. 3. Average weight of litter measured in a 20 cm diameter circle around each hardwood seedling. "nr" = no-regeneration samples. Error bars indicate standard error.
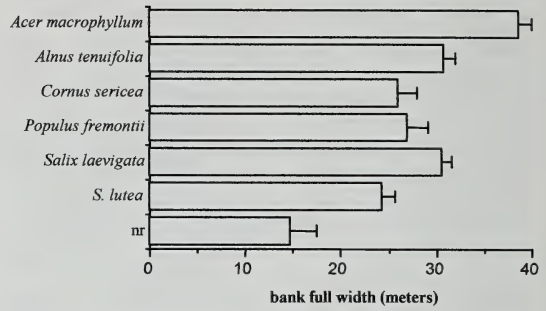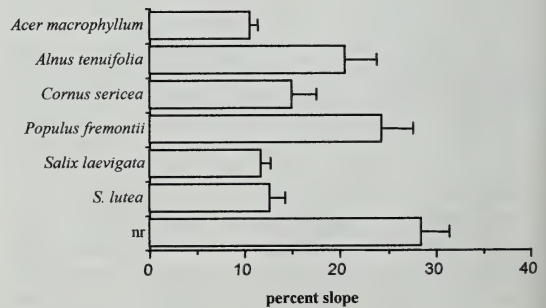

FIG. 5. Average percent slope measured at random sample points on three streams in the Sierra Nevada mixed conifer forest. "nr" = no-regeneration samples. Error bars indicate standard error.
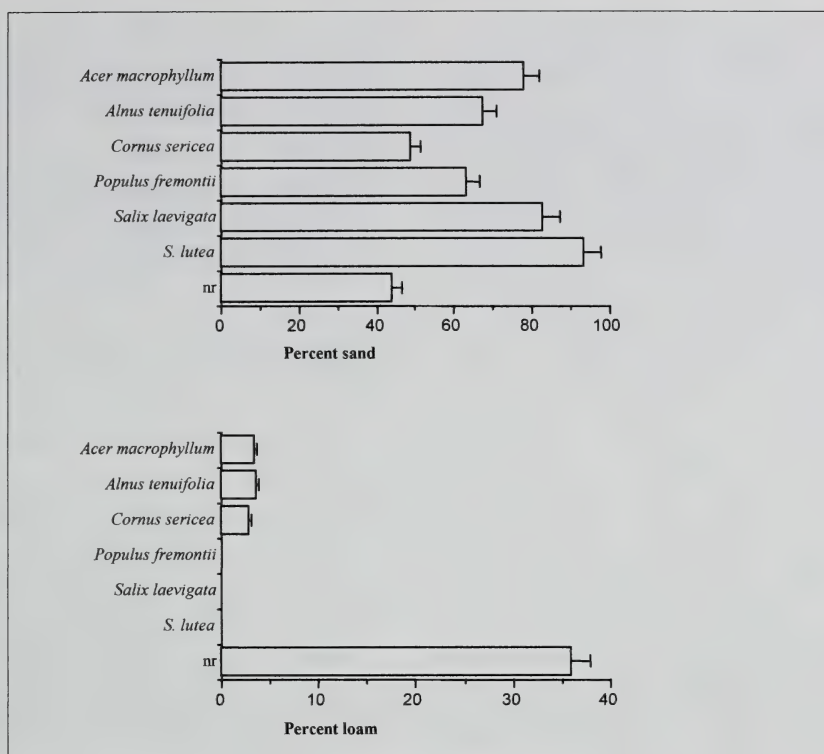
FIG. 6.   The relative frequency of soil texture (sand), and soil texture (loam), on points sampled on three streams in the Sierra Nevada mixed conifer forest. "nr" = no-regeneration samples. Error bars indicate standard error.

soil texture where hardwood seedlings occurred (Fig. 6). The highest frequencies of sand were measured for *S. laevigata* (F = 1.94, P < 0.001) and *S. lutea* (F = 8.75, P < 0.001), with *A. macrophyllum* (F = 8.75, P < 0.001), *A. tenuifolia* (F = 0.628, P = 0.005), and *P. fremontii* (F = 2.06, P < 0.001) following. The relative frequency of sand for *C. sericea* samples was not significantly different from the no-regeneration samples (F = 0.95, P = 0.157). In contrast, the highest frequency of loam soils was found at no-regeneration samples (Fig. 6). A small percentage of the soils where *A. tenuifolia*, *C. sericea*, and *A. macrophyllum* were found were classified as loam, and no *P. fremontii*, *S. laevigata* or *S. lutea* were found on loam soils.

DISCUSSION

The purpose of this study was to determine the environmental factors that are associated with the regeneration of hardwood species in the riparian woodlands of the Sierra Nevada mixed conifer forest. Results indicate a number of strong correlations between seedling density and these factors, but the requirements for recruitment were highly species dependent. The species sampled for this study can be divided into to broad categories based on the environmental conditions correlated with seedling establishment. The seedlings of *Acer macrophyllum*

and *Cornus sericea* were found under relatively high canopy, moderate sunlight environments suggesting that they were somewhat shade tolerant. The seedlings of *Alnus tenuifolia, Populus fremontii, Salix laevigata,* and *S. lutea* were found only in low canopy, high sunlight environments suggesting that they were shade intolerant. Both species of *Salix* and *A. tenuifolia* exhibited the greatest shade intolerance, while *P. fremontii* was more tolerant. This supports the conclusions of other researchers in regard to *P. fremontii* and other related species of cottonwood (Shafroth et al. 1995; Auble and Scott 1998; Stromberg 1998; Kalischuck et al. 2001).

A similar grouping was found in relation to litter weight. *A. tenuifolia* and *Salix* seedlings were generally found where litter weight was low. The most prevalent site for the occurrence of these seedlings was on sand bars and gravel bars. In contrast *P. fremontii, A. macrophyllum,* and *C. sericea* were able to regenerate on sites where litter accumulation was somewhat higher. Previous research has also indicated that bare mineral soil is the most advantageous substrate for the recruitment of riparian hardwood species (Auble et al. 1997).

The texture of soil substrate was also correlated with the recruitment of hardwood seedlings. Sediment composition has been found to affect the dis-

tribution of willows and cottonwoods through pre-
vious research (Merigliano 1998). Our data indi-
cates that all of the species sampled in this study
with the exception of *C. sericea* were found with
greater frequency on sites with a higher component
of sand in the soil. Similarly sites that had loam
soils were much less likely to host hardwood re-
cruitment. There were no examples of *P. fremontii,
S. laevigata,* or *S. lutea* recruitment on loam soils
on these study sites, and only a few examples of *A.
macrophyllum, A. tenuifolia,* and *C. sericea* recruit-
ment on the same soil type.

The height from stream and distance from stream
measures in this study were proxies for inundation
potential. Previous research has demonstrated that
inundation capacity can effect the distribution of
hardwood species (Scott et al. 1997; Mahoney and
Rood 1998; Amlin and Rood 2001; Roelle et al.
2001). Strong correlations were found between *A.
tenuifolia* and *S. laevigata* and height from creek,
and distance from creek indicating that inundation
potential has been a factor in their recruitment.

In general, *A. tenuifolia, S. laevigata* and *S. lutea*
exhibited the highest affinity for disturbed riparian
sites. *P. fremontii, C. sericea,* and *A. macrophyllum*
appear to play a more transitional role between the
open stream bank and the upland forest. However,
a general trend was observed in relation to the var-
iables measured. All of the species were more com-
mon on conditions that exist within the riparian
zone and result from repeated disturbance. These
conditions included mineral soils with a relatively
high content of sand, and low canopy cover with
resulting high light intensity. Other factors that
were correlated to seedling density some cases in-
cluded measures of proximity to riparian condi-
tions, including the height and distance from the
stream. The importance of these factors may be re-
lated to soil moisture, as was demonstrated in
McBride and Strahan (1984), or may be related to
the frequency of disturbance closer to the stream.
All of the species sampled occurred most frequently
on sites with relatively wide shallow stream chan-
nels. Stream channels that were narrow and steep
tended to be dominated by conifers. The conditions
that favor the recruitment of riparian hardwood spe-
cies are similar to those that favor hardwoods in
coniferous forests in general. Hardwoods tend to
dominate disturbed sites. Because of the dynamic
nature of fluvial processes stream banks experience
a relatively high frequency of disturbance. Recur-
rent flooding scours stream banks creating mineral
soil beds and reduces canopy cover through me-
chanical damage (Auble and Scott 1998). Where
riparian hardwoods differ from their upland hard-
wood counterparts is in their dependence on ripar-
ian conditions. These species are adapted to flood
through sprouting ability, and tolerance of inunda-
tion, but are also dependent on it to create the con-
ditions necessary for reproduction and establish-
ment (Scott et al. 1997).

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DEPTH DISTRIBUTION OF ARBUSCULAR MYCORRHIZAE ASSOCIATED WITH MESQUITE

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ABSTRACT

Prosopis glandulosa (Mesquite), an arbuscular mycorrhizal (AM) species, is the dominant tree of the Apacherian savanna of southeast Arizona and is characterized by a very deep root system. A corn bioassay was used to examine the mycorrhizal inoculum potential (MIP), or the amount of AM propagules, at 10 cm depth intervals in 1 m deep soil pits adjacent to mesquite trees across two seasons. MIP was found to be lowest in the caliche layer of the soil, increasing above and below this depth. AM spore densities showed a trend of decreasing with depth but there was no discernable trend in AM colonization of mesquite roots. Both MIP and spore densities were higher in the fall than in the spring.

Key Words: arbuscular mycorrhizae, mesquite, Apacherian Savanna, seasonality, mycorrhizal inoculum potential.

Arbuscular mycorrhizae (AM) are important components of virtually all terrestrial ecosystems. Over 90% of all higher plants are estimated to be mycorrhizal, and >80% of these form AM relationships (Brundrett 1991). Plant growth is generally enhanced by this association, mainly due to an increased ability to take up nutrients, principally phosphorus (Mullen and Schmidt 1993; Smith and Read 1997) and nitrogen (Tobar et al. 1994). The mutualism also enhances plant host drought resistance (Davies et al. 1992), competitive ability (West 1997a; Titus and del Moral 1998), and resistance to fungal pathogens (West 1997b) and insect herbivores (Gange and Bower 1997).

Many studies have found that seasonal factors, which are related to the developmental stage of the host plant and to environmental conditions play a major role in AM colonization levels (e.g., Mullen and Schmidt 1993; Sanders 1993; LaPointe and Molard 1997; Bohrer et al. 2001). Temporal factors may also play a role in host benefit from AM colonization. For example, AM may only benefit plants during the brief periods when phosphorus demand is high during fruit production (Fitter 1989; Sanders and Fitter 1992a).

The arbuscular mycorrhizal mutualism is considered to be critical to the survival of most plants in arid environments. Perennial plants in undisturbed arid environments have generally been found to be mycorrhizal (e.g., Trappe 1981; Bloss 1985; Siguenza et al. 1996; Carrillo-Garcia et al. 1999; Stutz et al. 1999). However, the mycorrhizal status of most desert species, the distribution of mycorrhizal fungal propagules with depth, and how the level of colonization shifts over the seasons remains little

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known. It has been found that mycorrhizal colonization in a semi-arid system was higher towards the end of summer than in midwinter (Requena et al. 1996).

Prosopis glandulosa (Mesquite), a mycorrhizal species, is the dominant tree of the Apacherian savanna or semiarid grassland of southeast Arizona and is characterized by a very deep root system (Burgess 1995). Mesquite, a nitrogen-fixing legume, is important in maintaining the long-term productivity of Southwestern desert ecosystems (Virginia and Jarrell 1983). This study was conducted in order to characterize mycorrhizal inoculum potential (MIP), the amount of mycorrhizal propagules (spores, hyphae and mycorrhizal root fragments) in the soil that can colonize a plant, across a depth gradient and seasons in soil adjacent to mesquite trees. The density of AM spores in the soil and the mycorrhizal colonization of mesquite roots were also assessed.

METHODS

Our study took place September 2000 to December 2001 in ungrazed Apacherian savanna (Sonoran desert grassland) at Columbia University's Biosphere 2 Center, 42 km north of Tucson, Arizona (32°34'44.0"N, 110°50'52.2"W). Elevation is 1182 m and average annual precipitation 51 cm/yr. Apacherian savanna is characterized by mesquite *P. glandulosa,* grasses, cacti, and shrubs. The soil is an aridisol defined by clay at the surface and caliche below. Caliche is a layer of soil in which the soil particles have been cemented together by calcium carbonate. The caliche on the Biosphere 2 Campus is Pleistocene in age and has weathered into a clay. Three 1 m deep soil pits, 20–50 m apart and immediately adjacent to mature mesquite trees, were excavated in fall 2000. The caliche layer be-

gan at 30–40 cm deep and ended at 80–90 cm deep depending upon the pit.

In spring and fall 2001, 1.2 kg soil samples were collected at 10 cm increments in the three soil pits. The spring collections were collected and processed simultaneously but soil samples from one of the soil pits were collected and processed 3 months after the other two holes in the fall collection. Within 2 weeks after collection soil was sieved through a 2 mm sieve and three 350 ml replicate soil samples from each of the ten 10 cm depth increments from each of the three soil pits were placed in plastic 10 cm diameter square pots. Soil was amended with 100 ml perlite to maintain drainage, and planted with three non-fungicide treated *Zea mays* seeds. This yielded a total of 90 pots. Corn seedlings were thinned to one per pot after one week. Mycorrhizal inoculum potential (MIP) is a bioassay index of the quantity of inoculum in the soil as measured by the percent AM fungal colonization of corn roots (Moorman and Reeves 1979; Titus et al. 1998). All pots were watered daily with tap water. Fertilizer was applied in 50 ml aliquots per pot of 10% Hoaglands solution minus phosphorus at biweekly intervals throughout the experiment. The control consisted of 8 pots of sterile soil placed randomly among the 90 treatment pots and planted with corn to determine if contamination by glasshouse AM propagules occurred. Pots were randomized and maintained for 42 days at a Biosphere 2 Campus glasshouse facility at 23–28°C, and rotated every 15 days. For each sample, percent colonization of the three corn plants were averaged together to achieve MIP for each depth in each soil pit.

In order to determine the extent of AM colonization of mesquite at different depths fine roots were collected across the depth gradient in spring and fall 2001. Roots could not be found at every depth increments in each pit. Roots were placed into plastic bags, frozen and subsequently assessed for the three AM structures, hyphae, vesicles and arbuscules.

Roots were washed, cleared and stained with trypan blue (Brundrett et al. 1994). Percent AM colonization of fine roots (<1 mm in diameter) was estimated by placing a grid of 1 cm squares below a petri plate that contained the root sample under a dissecting microscope. Fifty locations in which a root crossed a line on the grid were scored for AM colonization in the corn roots and for hyphae, arbuscules and vesicles in the mesquite roots. Many samples were examined under higher power to ascertain that the structures were indeed AM. The number of mycorrhizal "hits" is used as an estimate of percent root colonized by the three AM structures (Brundrett et al. 1994).

Each soil sample was also used to determine spore populations across the depth gradient in fall 2000 and spring 2001. For each sample, two 10 ml samples were blended with water in an electric blender and sieved through 250 um and 63 um

TABLE 1. REPEATED MEASURES ANOVA F AND P VALUES FOR MYCORRHIZAL INOCULUM POTENTIAL (MIP) AND SPORE DENSITIES FROM SOIL ADJACENT TO MESQUITE TREES COLLECTED AT 10 CM DEPTH INCREMENTS ACROSS TWO SEASONS IN APACHERIAN SAVANNA IN 2001 (n = 3, $P \leq 0.05$ FOR SIGNIFICANCE, DATA ARC-SINE TRANSFORMED).

Variable	MIP		Spores	
	F	P	F	P
Season	73.779	0.000	5.939	0.024
Depth	5.029	0.001	2.790	0.027
Interaction	2.592	0.036	0.527	0.838

sieves to eliminate both clays and coarse materials. The remaining material on the sieve was then washed onto filter paper using a funnel and examined under a dissecting microscope for AM spores. For each sample, spore densities from the two subsamples were averaged to achieve the density of spores per 10 g of soil. Spores were preserved on slides in both polyvinyl alcohol glycerol and Melzer's solution (Morton et al. 1993). Spores were determined to be AM fungi but identification to genera were problematic due to natural decay processes.

For each season MIP levels were arc sine transformed for increased normality and homogeneity of variances and contrasted by repeated measures ANOVA at $\alpha = 0.05$. Post-hoc tests were conducted by Tukey's honestly significant difference test. Spore densities were also contrasted by repeated measures ANOVA at $\alpha = 0.05$. Mesquite root AM colonizations were not compared statistically due to sample size.

RESULTS

Repeated measures ANOVA found MIP levels significantly greater in the fall than in the spring, significantly different across depths, and a significant interaction between season and depth (Table 1, Fig. 1). By Tukey's post-hoc test the surface soil (0–10 cm depth) was found to have a significantly greater MIP than caliche soils at 60–90 cm. Spore densities were greater in fall than in spring and surface soils were found to have more spores than deeper soils (Table 1, Fig. 2). A non-significant trend for an increase in both MIP and spore densities below the caliche at 90–100 cm was evident.

Mesquite roots could not be found at many of the 10 cm depth increments, therefore sample sizes varied. AM colonization was found in all mesquite roots collected (Table 2). Vesicles and arbuscules were infrequent. There was a weak trend for AM colonization to decrease with increasing depth and most of the mesquite roots, particular at greater depths, increased in AM colonization from spring to fall. The three indicators of AM, i.e., spore densities, root colonization and MIP, were not correlated (Table 3).

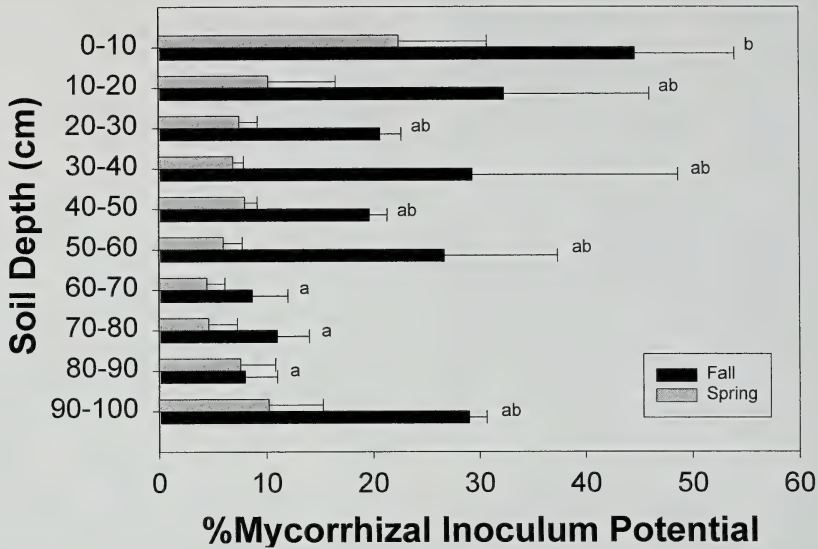# Mycorrhizal Inoculum Potential across Soil Depth and Season

Fig. 1. Mean percent mycorrhizal inoculum potential at 10 cm depth increments adjacent to mesquite trees in spring 2001 and fall 2001 in Apacherian Savanna (n = 3, ± one standard deviation). Repeated measures ANOVA found at $P \leq 0.05$ greater spore densities in the fall than in the spring and greater spore densities in surface soils than in deeper soils. Depth increments with different superscripts were found to have different spore densities by Tukey's post-hoc test. See Table 1 for repeated measures ANOVA F's and P's.

DISCUSSION

Because most perennial arid zone plants in undisturbed environments are AM (Trappe 1981; Bloss 1985; Carrillo-Garcia et al. 1999; Titus et al. 2002), positive MIP values in soil adjacent to mesquite would be expected. In arid zones, MIPs vary seasonally, spatially and in relation to environmental variables (Al-Agely and Reeves 1995; Requena et al. 1996; Titus et al. 2002, in press), as in more mesic environments (Johnson et al. 1991b; Brundrett et al. 1996). In this study MIP varied significantly with season and depth. The large standard deviations also show that MIP varied between the three soil pits. The depth to the beginning of the caliche layer differed slightly between holes, varying from 30–40 cm, however, the major decrease in MIP was between 60–90 cm in the fall and low MIP values were found across a much broader range in the spring with the lowest values at 60–80 cm depth. A decrease in MIP in the caliche may be because roots and hyphae cannot penetrate the hard caliche layer. Caliche is more broken in the upper regions because of the greater number of roots in these layers, which may be the reason MIP is greater in the upper caliche. The trend of a decrease in AM mycorrhizal colonization of mesquite roots with depth may be due to the decrease in MIP or to a scarcity of available soil nutrients in the

caliche layer. Because of a lack of available nutrients in the caliche hyphae may not proliferate inside mesquite roots at these depths. The paucity of vesicles and arbuscules may indicate that little interaction is occurring between the fungi and the mesquite at the collection times.

Fungal spore densities are low in arid soils, and zero counts are common (Cui and Nobel 1992; Siguenza et al. 1996; Requena et al. 1996; Carrillo-Garcia et al. 1999; Titus et al. in press). Spores have been been found to be located <50 cm deep in some arid soils (Al-agely and Reeves 1995; Stutz and Morton 1996; Stutz et al. 1999), but much deeper in other arid soils (White et al. 1989). AM colonized mesquite roots have been found 4.5–4.8 m deep in the Sonoran Desert (Virginia et al. 1986). Arid zone AM fungal species may only sporulate infrequently in response to a period of favorable temperature and moisture (Stutz and Morton 1996; Stutz et al. 1999). Stutz and Morton (1996) and Stutz et al. (1999) found that by using three successive cycles of trap cultures of Sonoran and Chihuahuan soils from mesquite roots they greatly increased spore density and species richness to a level approaching that of mesic environments.

The increase in MIP and spore density from spring to fall may be due to a host of variables, such as climatic and temporal factors. Why this in-

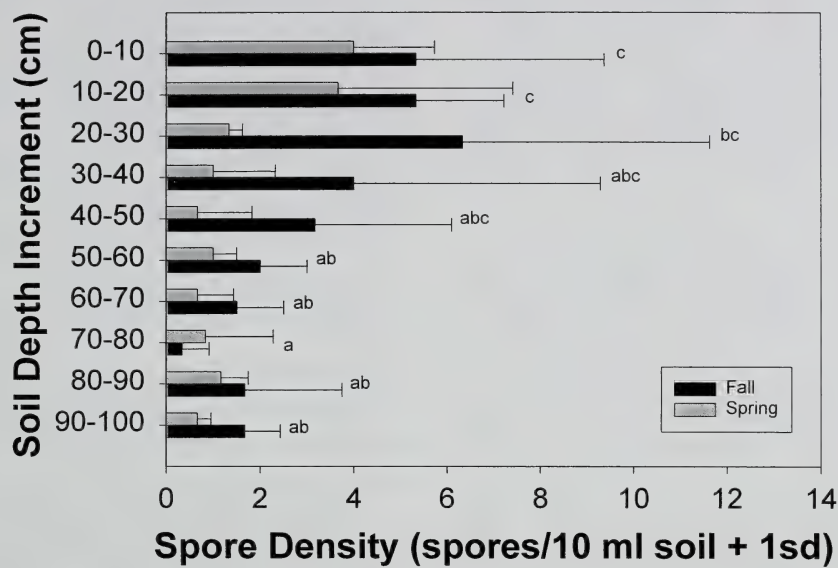# Arbuscular Mycorrhizae Spore Density across Soil Depth and Season

FIG. 2.   Arbuscular mycorrhizal spore densities at 10 cm depth increments in soil adjacent to mesquite trees in spring 2001 and fall 2000 in Apacherian Savanna (n = 3, ± one standard deviation). Repeated measures ANOVA found at P ≤ 0.05 greater spore densities in the fall than in the spring and greater spore densities in surface soils than in deeper soils. Depth increments with different superscripts were found to have different spore densities by Tukey's post-hoc test. See Table 1 for repeated measures ANOVA F's and P's.

crease in MIP occurred in this study is unknown. AM colonization of plant roots have been found to decrease from spring to fall perhaps because of a decrease in plant phosphorus demand although this will vary with soil moisture and rates of root growth and turnover (Titus and Leps 2000; Ruotsalainen et al. 2002). For example, AM root colonization has been found to be lowest in early summer due to rapid root growth outstripping the spread of AM colonization (Douds and Chaney 1982; Warner and Mosse 1982; Dickman et al.

1984; Ebbers et al. 1987). AM levels of plant roots have also been found to be unchanged across seasons (Titus et al. in press). The trend in AM colonization of the mesquite roots in this study was to increase from spring to fall at the lower depths.

Indices of AM, MIP, spore counts and root colonization are often not correlated (e.g., Ebbers et al. 1987; Scheltma et al. 1987; Johnson et al. 1991a; Titus et al. in press), as was the case in this study. Spore counts assess only one type of AM propagule, MIP indirectly measures all types, i.e.,

TABLE 2.   ARBUSCULAR MYCORRHIZAL HYPHAE, VESICLE AND ARBUSCULE LEVELS OF MESQUITE (*PROSOPIS GLANDULOSA*) ROOTS COLLECTED AT 10 cm DEPTH INCREMENTS ACROSS TWO SEASONS IN APACHERIAN SAVANNA IN 2001 (n = 1, 2 OR 3, ± ONE STANDARD DEVIATION).

Depth (cm)	Spring			Fall		
	Hyphae	Vesicles	Arbuscules	Hyphae	Vesicles	Arbuscules
0–10	32 ± 18	2 ± 2	2 ± 3	26 ± 14	2 ± 0	2 ± 2
10–20	16 ± 12	1 ± 1	3 ± 2	16 ± 10	0 ± 0	3 ± 5
20–30	10 ± 4	0.6 ± 0.6	0 ± 0	44 ± 14	1 ± 2	0 ± 0
30–40	6 ± 4	0 ± 0	0 ± 0	37 ± 16	2 ± 2	2 ± 3
40–50	16 ± 9	0.3 ± 0.6	1 ± 1	19 ± 13	1 ± 2	0 ± 0
50–60	6 ± 3	1 ± 0	0 ± 0	15	0	0
60–70	6	0	0	10	0	0
70–80	8 ± 4	0 ± 0	0 ± 0	22	2	2
80–90	4	0	0	12 ± 8	0 ± 0	0 ± 0
90–100	2	0	2	8	0	0

TABLE 3. SPEARMAN'S RANK CORRELATION P VALUES BE-TWEEN MEAN MYCORRHIZAL INOCULUM POTENTIAL (MIP), ARBUSCULAR MYCORRHIZAL (AM) SPORE DENSITIES, AND AM COLONIZATION OF MESQUITE ROOTS IN THE SPRING AND FALL. The three indicators of arbuscular mycorrhizae were not correlated at P < 0.05.

	Spring		Fall	
	MIP	Spores	MIP	Spores
Mesquite AM	0.254	0.153	0.347	0.309
Spores	0.191		0.841	

spores, hyphae and AM colonized roots, and root colonization is a snap-shot in time of the AM colonization of fine roots. Different AM species do not sporulate to the same degree, at the same time, or in response to the same environmental variables across a wide range of environments (Siguenza et al. 1996; Stutz and Morton 1996; Allen et al. 1998; Stutz et al. 1999). Host species, surrounding vegetation, soil, and climatic and temporal factors are likely to influence AM root colonization levels (Johnson et al. 1992; Sanders and Fitter 1992b; Blaszkowski 1994; Titus and del Moral 1998). Thus, because of the large number of variables that influence AM indicators, a lack of correlation is not surprising.

This study increases our understanding of the distribution of AM with soil depth in a mesquite dominated environment. Mycorrhizae are critical to the procurement of essential nutrients for mesquite and other arid zone desert plants for at least part of their life cycle, thus, an understanding or the distribution of AM can help understand the dynamics of the mutualism. Further research is needed to understand the mechanisms behind the seasonal and depth AM distributions observed in this study.

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EDAPHIC DIFFERENTIATION IN *LASTHENIA*: A MODEL FOR STUDIES IN EVOLUTIONARY ECOLOGY

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ABSTRACT

The current knowledge of the goldfield genus *Lasthenia* is discussed, emphasizing the possible role of edaphic factors in the divergence of this predominantly Californian genus. *Lasthenia* species occupy a wide array of edaphic habitats ranging from serpentine outcrops to salt flats to guano deposits, thriving under specific ion and osmotic conditions that are uninhabitable for the vast majority of species. Studies show that ion accumulation and sequestration are common strategies used to counter osmotic effects, common to most habitats harboring *Lasthenia* species. Inter- and intra-specific variation in tolerance to edaphic conditions has been observed in closely related yet reproductively isolated taxa, suggesting that edaphic factors may have set the stage for the diversification of this genus. *Lasthenia* provides numerous opportunities to examine the link between adaptation, reproductive isolation and speciation.

Key Words: adaptive divergence; California flora; edaphic races; *Lasthenia*; salinity tolerance; serpentine.

According to Lindley and Moore (1876), "they (*Lasthenia*) grow in wet places, and appear to be uninteresting weeds." They do "grow in wet places," but studies of *Lasthenia* (Heliantheae: Asteraceae) over the last several decades have shown the genus to consist of anything but "uninteresting weeds." Commonly known as goldfields, plants of *Lasthenia* occupy large areas of the Californian landscape, casting spectacular carpets of brightly-colored golden yellow flowers in early spring. A recent molecular phylogenetic study recognized 21 species and subspecies belonging to seven sections (Chan et al. 2001). All but one species are endemic to the Californian Floristic Province. *Lasthenia kunthii* (Less.) Hook & Arn., the only member of the genus found outside western North America, is endemic to vernal pools and wetlands in central Chile (Ornduff 1966). Members of the genus have wide edaphic tolerance and are found in habitats such as coastal bluffs, guano deposits, vernal pools, salt and alkaline flats, serpentine outcrops, deserts, grasslands, and open woodlands (Ornduff 1966, 1993). Members of *L. californica sensu* Ornduff (Ornduff 1993) have the widest edaphic tolerance within the genus, with populations spanning all but guano habitats. Keck (1959) stated that *L. californica sensu* Ornduff [then *Baeria chrysostoma* (Fischer & C. Meyer) E. Greene] was the most abundant composite in California. Other *Lasthenia* taxa have rather restricted distributions, with seven taxa now listed in California Native Plant Society's "Inventory of Rare and Endangered Plants of California" (CNPS 2001).

Following Ornduff's extensive monograph (1966), *Lasthenia* has received considerable attention. Early studies examined inter- and intra-specific variation in flavonoid chemistry (Saleh and Bohm 1971; Ornduff et al. 1973, 1974; Bohm et al.

1989; Desrochers and Bohm 1993) to assess biosystematic relationships and determine trends of biochemical evolution in the genus. Electrophoretic work followed to establish evolutionary relationships among closely related taxa within the genus (Crawford et al. 1985; Crawford and Ornduff 1989) as well as within the highly variable *L. californica sensu* Ornduff (Desrochers and Bohm 1993). More recently, comprehensive phylogenetic studies (Chan et al. 2001, 2002; Desrochers and Dodge 2003) have contributed to our understanding of patterns of divergence in *Lasthenia*. The study by Chan et al. (2001) agrees with observations made earlier (Ornduff 1966, 1976) that divergence patterns in the genus conform to expectations of catastrophic selection and saltational diversification (Lewis 1962).

Existing knowledge suggests that *Lasthenia* can provide a model system for studies in evolutionary ecology, specifically, in understanding the role of edaphic factors in differentiation. Species of *Lasthenia* have successfully colonized diverse habitats within California, including those that exclude the vast majority of species (Ornduff 1966, 1993; Kingsbury et al. 1976; Vasey 1985; Rajakaruna and Bohm 1999; Noe and Zedler 2000; Parsons and Whelchel 2000). Further, in some sections (e.g., sect. *Hologymne* [Bartling] A. Gray and sect. *Ornduffia* R. Chan) all species occupy the same edaphic habitat yet generally do not grow intermixed (Ornduff 1966), while in others (e.g., sect. *Ptilomeris* [Nutt.] Ornduff), species occupy contrasting edaphic habitats (Crawford et al. 1985; Vasey 1985). Thus it is plausible to hypothesize that edaphic factors may have played an important role in the diversification of the genus. In this paper, taxa in several sections are discussed with emphasis on the

possible role of edaphic factors in their diversification. Since many endemic species of flowering plants in western North America are edaphic endemics (Kruckeberg 1969, 1986), studies of a model genus such as *Lasthenia* could provide general insights into speciation in a variety of other such edaphically diverse genera.

Lasthenia sect. *Amphiachaenia* (DC.) R. Chan: *L. californica sensu* Ornduff

Lasthenia sect. *Amphiachaenia,* formerly known as *L.* sect. *Baeria* (Fisch. & Mey.) Ornduff, was recently revised (Chan 2001) to include four species, *L. californica* DC. ex Lindl. [consists of subsp. *californica,* subsp. *macrantha* (A. Gray) R. Chan, and subsp. *bakeri* (J. T. Howell) R. Chan], *L. gracilis* (DC.) Greene, *L. ornduffii* R. Chan, and *L. leptalea* (A. Gray) Ornduff. *Lasthenia californica* and *L. gracilis* were previously recognized as *L. californica sensu* Ornduff (1993). The two cryptic taxa found within *L. californica sensu* Ornduff, *L. californica* subsp. *californica* and *L. gracilis,* have been the subject of intense ecological and evolutionary studies (Rajakaruna and Bohm 1999; Chan et al. 2002; Desrochers and Dodge 2003).

A biosystematic study (Desrochers and Bohm 1995) first suggested the existence of two geographical races within *L californica sensu* Ornduff based on flavonoid pigments (Bohm et al. 1989; Desrochers and Bohm 1993), allozyme banding patterns, and cypsela characteristics. A detailed ecological study (Rajakaruna and Bohm 1999) suggested that the two races described by Desrochers and Bohm (1995) occur in distinct sets of habitats that can be classified on the basis of ionic stresses and water availability. Race A plants predominate in habitats subject to ionic stress. Although the soils in these environments are ionically harsh, the percent clay content is generally high, increasing the water holding capacity of the soil. Plants are often restricted to moist or even saturated soils in such environments. In contrast, race C plants are found in ionically "benign" inland environments. The soils are often sandy, rocky, and shallow, drying out early in the growing season. The conditions at Jasper Ridge Biological Preserve (Stanford University, San Mateo Co., CA), where the races occur in parapatry, mirror the trends seen across the range of the taxa, with the two races occupying distinct microhabitats: Race A occupying the wet, yet ionically harsh soils at the bottom of the serpentine ridge, while race C occupies the fast-drying, yet ionically less stressful upper reaches (Rajakaruna and Bohm 1999). At Jasper Ridge, race A plants belong to *L. californica* subsp. *californica* while race C plants belong to *L. gracilis.* However, the races do not always correspond to the two taxa recognized by Chan et al. (2001, 2002). A recent study shows that one or both edaphic races have evolved in parallel in both *L. californica* subsp. *californica*

and *L. gracilis,* suggesting that racial features may have evolved secondarily in response to edaphic factors (Rajakaruna et al. in press a).

Recent eco-physiological studies (Rajakaruna et al. 2003) indicate that race A plants from both *L. californica* subsp. *californica* and *L. gracilis* are clearly more tolerant of potentially-toxic Na^+, suggesting that physiological traits responsible for Na^+ uptake and sequestration may have evolved independently in populations belonging to the two closely related taxa. Schat et al. (1996) provide one of the best examples of parallel genotypic changes in tolerance to an edaphic extreme within a plant species. Their studies have shown that loci confering copper tolerance have evolved independently in geographically isolated populations of *Silene vulgaris* Garcke (Caryophyllaceae). In *Plantago* (Plantaginaceae), the vacuolar Na^+/H^+ antiporter activity, thought to confer tolerance to Na^+ (Apse et al. 1999) is only present in the salt-tolerant *P. maritima* L. but not in the glycophytic *P. media* L. (Staal et al. 1991). This difference is thought to be crucial in the ecological divergence of these two species. Sodium is clearly an important element in many of the habitats where race A is found. Whether the presence/absence or level of expression of the Na^+/H^+ antiporter gene is responsible for the differences in uptake and accumulation in race A plants is an area worthy of investigation. Ion uptake studies conducted on the two races from Jasper Ridge also indicate that race A is more tolerant of high external Mg^{2+} and low Ca^{2+}/Mg^{2+} ratios (Rajakaruna et al. 2003). Both of these traits have adaptive significance in magnesium-rich serpentine and coastal habitats where race A is found. The traits that have been studied (Na^+, Mg^{2+}, Ca^{2+}/Mg^{2+}) are common features in most habitats where race A is found, thus, it is tempting to hypothesize that differential response to edaphic stresses may have played an important role in the racial divergence of *L. californica sensu* Ornduff. By extending eco-physiological studies to characterize the physiology of hybrids between the two species (and races), it is possible to appreciate better the role of edaphic factors in diversification.

The findings from ecophysiological studies (Rajakaruna et al. 2003) suggest a correlation between flavonoid differences, edaphic features, and ion accumulation, suggesting a previously unknown adaptive role for flavonoid differences. The primary feature that distinguishes the edaphic races in *L. californica* subsp. *californica* and *L. gracilis* is the flavonoid pigment profile; race A contains sulfated compounds, namely sulfated kaempferol and quercetin diglycosides plus prominent eriodictyol glycosides (Bohm et al. 1974, 1989; Desrochers and Bohm 1993) not found in race C plants. Ecological roles for flavonoid pigments have often been postulated (Bohm 1987), and the case for a correlation with habitat and sulfated flavonoids has been brought forward (Harborne 1975). A large number

of taxa found in habitats with water logged and saline conditions contain sulfated flavonoids (Harborne 1975; Barron et al. 1988). In *L. californica* subsp. *californica* and *L. gracilis,* sulfated flavonoids occur only in Na+-accumulating plants that predominate in ionically-stressed environments. It is possible that sulfation of flavonoids may be beneficial in sulfate-rich environments where race A occurs. Thus, Rajakaruna et al. (2003) hypothesized an edaphically-linked ecological role for the flavonoid differences that first suggested the existence of these two races (Bohm et al. 1974, 1989).

A study on the response to water stress suggests that the two races from Jasper Ridge show different life history strategies in response to water stress (Rajakaruna et al. in press b). Race C plants (*L. gracilis*) adopt a drought avoidance strategy often referred to as phenological escape (Fox 1990; Aronson et al. 1992) and have significantly greater relative fitness than race A plants under increasing water stress. In contrast, race A plants (*L. californica* subsp. *californica*) adopt a slow-growing strategy and allocate more biomass to root than shoot. This strategy is commonly seen in herbaceous annuals growing under edaphic stress, specifically under water and nutrient stresses (Kramer 1980; Grime 1994). Since the study was conducted in potting soils, to seek effects of water stress in isolation, it is unclear how the findings relate to conditions experienced in the field. A large-scale experiment using natural soils is required to clarify further the relationship between ionic strength, water availability and fitness within environments, and to further explore factors that affect the distribution of these races at Jasper Ridge and across the species' range. Given our understanding of the environmental variables associated with differences in fitness, it is now possible to conduct detailed analysis of selection gradients (Wade and Kalisz 1990; Dudley 1996) to infer the role of natural selection in achieving fitness differences under field conditions.

Previous studies (Desrochers 1992) suggested low crossability as well as reduced gene flow between races (Desrochers and Bohm 1995) of *L. californica sensu* Ornduff. A recent study using seven populations of *L. californica* subsp. *californica* and *L. gracilis* show reduced crossability between the two closely related cryptic taxa (Rajakaruna and Whitton unpublished). Examination of intra- and inter-racial seed set as an effect nested within species suggests that the edaphic races are also reproductively isolated. By comparing patterns of seed set with observations of pollen tube growth, it is clear that most of the reduction in seed set is due to post-pollination, prezygotic effects. Interestingly, there is evidence for enhanced prezygotic isolation in the parapatric location at Jasper Ridge. This pattern suggests a possible role for reinforcement in the observed isolation. Flowering times have diverged in the parapatric location with *L. gracilis* plants always flowering 7–10 days prior to *L. cal-*

ifornica subsp. *californica* plants; the pattern is maintained in the greenhouse. Germination tests also revealed evidence for reduced hybrid fitness. Strong ecological selection at the site (Rajakaruna and Bohm 1999) may severely limit introgression. The fate of any hybrids produced is unknown. A transplant study of hybrids in parental habitats would shed light on possible post-zygotic mechanisms of isolation. Further studies are needed to clarify the roles of ecological selection versus reinforcement on the patterns of reproductive isolation observed between races and the two cryptic plant taxa.

An understanding of the relationship between traits for adaptation and reproductive isolation is critical to further the hypothesis of edaphic differentiation in *L. californica* subsp. *californica* and *L. gracilis*. Studies suggest that reproductive isolation can be achieved as a by-product of a physiological adaptation to unusual soil conditions (Macnair and Gardner 1998). Macnair and colleagues have shown that the linkage block associated with copper tolerance in *Mimulus guttatus* Fischer ex DC. (Scrophulariaceae) also produces hybrid inviability; however, it is unclear if inviability is achieved via pleiotropy or hitchhiking. Nevertheless, their work has clearly documented that natural selection for an adaptive trait (copper tolerance) has caused a gene for post-zygotic isolation to spread through the population (Macnair and Christie 1983; Christie and Macnair 1987). Whether such relationships exist between edaphic tolerance and observed reproductive isolation in *L. californica sensu* Ornduff is worthy of investigation.

Lasthenia sect. *Ptilomeris* (Nutt.) Ornduff: *L. minor* and *L. maritima*

Lasthenia minor (DC.) Ornduff occurs in a variety of habitats such as alkali flats, coastal bluffs, sand dunes, pond margins, and disturbed sites while *L. maritima* (A. Gray) M. Vasey is restricted almost exclusively to islands and offshore rocks harboring seabird nesting and roosting sites (Ornduff 1965, 1966; Vasey 1985). The soils on these sites are high in nitrogen, low in pH, and highly disturbed from the activities of the birds (Vasey 1985). In addition, constant wind and salt spray produce an outright hostile environment.

Ornduff (1966) considered the self-compatible *L. maritima* to be a recent descendent from the self-incompatible *L. minor*. An electrophoretic study (Crawford et al. 1985) further supported this hypothesis and suggested that speciation probably involved a switch to self-compatibility, development of autogamy, and subsequent divergence driven by edaphic factors. Given that variation for tolerance is first required to colonize the extreme guano habitats, it is likely that self-compatibility arose post-colonization. Whether the switch to self-compatibility arose as a by-product of an adaptation to gua-

no or is directly linked to a gene conferring adaptation is not known.

A recent phylogenetic study (Chan et al. 2001) showed a close relationship between the two species, but it did not conclusively support the proposed ancestor-descendent relationship. The close relationship between the two species is reflected by the high fertility of artificial crosses (Ornduff 1966). However, Vasey (1985) reports that at the only truly sympatric site known for the two species, only a few plants appear to be intermediates. Examination of parapatric populations of the two species at three localities failed to reveal any indication of natural interspecific hybridization (Vasey 1985). It is possible that strong ecological selection is responsible for limiting introgression.

The physiological basis for the substrate tolerance in *L. maritima* is not known. Preliminary studies by Vasey (1985) show that *L. minor* is not tolerant of guano-modified soils. However, it is possible that extensive screening may reveal tolerant individuals among populations of this species. Such studies are critical to our understanding of the origin of *L. maritima*. Limited work suggests that *L. maritima* accumulates nitrates in its foliage (Ornduff 1965), and Vasey (1985) suggests that high nitrate content in the cells may have allowed *L. maritima* to grow in these osmotically-challenged sites. Nitrate uptake has been well characterized (Tischner 2000), and it is feasible to determine in the laboratory whether physiological differences exist between the two species in this regard. Other physiological differences between the two species, such as tolerance to excess cations such as Na^+ and high osmotic stress, also common to these sites, have not been examined. Clearly, there is much work to be done to assess mechanisms of tolerance to guano soils and the *L. maritima-L. minor* complex provides an ideal opportunity to do so. Once trait differences are established between the two species and their adaptive significance determined, it will be possible to examine their genetic basis. Whether traits contributing to adaptation to guano soils also contribute to isolation (i.e., self-compatibility or reduced hybrid fitness) can then be examined.

Lasthenia sect. *Hologyme* (Bartling) A. Gray:
L. chrysantha, L. glabrata, and *L. ferrisiae*

All three species in this section occupy saline habitats and form vigorous, moderate to highly fertile artificial hybrids (Ornduff 1966). Hybrid speciation was suspected in the origin of *L. ferrisiae* Ornduff, putatively from hybridization between *L. glabrata* Lindl. subsp. *coulteri* (A. Gray) Ornduff and *L. chrysantha* (Greene ex A. Gray) Greene (Ornduff 1966). The study by Chan et al. (2001) show minimal molecular variation for species within this section and is uninformative on the possible hybrid origin of *L. ferrisiae*. An interesting observation made by Ornduff (1966) is that these three closely related species, with edaphic requirements that appear to be identical, are never sympatric. A pure population of one of these species may exist within a few meters from a pure population of another. Ornduff (1966) attributes this pattern to occupation of a site on a "first come, first served" basis, yet admits that a detailed ecological study probably would reveal factors that are different among such sites. It is likely that the three taxa differ in their tolerance regime to edaphic features associated with salinity. The species-trio provides yet another setting to explore the relationships among adaptation, reproductive isolation, and diversification.

Lasthenia sect. *Ornduffia* R. Chan:
L. fremontii, L. conjugens, and *L. burkei*

All three species in this section are inter-crossable (Ornduff 1966, 1969). The ranges for *L. conjugens* Greene and *L. fremontii* (Torr. ex A. Gray) Greene marginally overlap, however, natural hybrids between the species are very rare (Ornduff 1969). Artificial hybrids between *L. conjugens* and *L. fremontii* show remarkable similarity to *L. burkei* (Greene) Greene, leading Ornduff (1966) to suggest a hybrid origin for this taxon. *Lasthenia burkei* occurs in vernal pool habitats similar to those occupied by its two relatives, but its geographical range is distinct. Many research tools have been utilized (Saleh et al. 1971; Crawford and Ornduff 1989; Chan et al. 2001) to resolve relationships within this section but have not been able to support conclusively Ornduff's hypothesis for the hybrid origin of *L. burkei*.

Although all three species colonize vernal pools, their distributional pattern within a pool seems to be related to water level, soil moisture, and salinity (Ornduff 1966). Ornduff (1966) claimed a similar situation to that described for the three halophytes in sect. *Hologymne,* where the species are rarely sympatric although they may be occupying sites just a few meters apart. Again, specific edaphic tolerances may exist among these vernal pool taxa and the sites they are restricted to may in fact show micro-scale differences in edaphic features. Only a close examination of these sites, such as our detailed study of the serpentine outcrop at Jasper Ridge (Rajakaruna and Bohm 1999), will reveal patterns of soil heterogeneity in these apparently uniform edaphic habitats. In a study conducted in an artificial vernal pool created at Berkeley, Ornduff (1966) demonstrated that *L. conjugens* was always restricted to the soil immediately above and below the water level while *L. fremontii* occurred from water level to the upper limit of soil moisture (Ornduff 1966). *Lasthenia conjugens* appeared to be the more water-dependent of the two species and may be occupying deeper vernal pools that dry out later in the growing season. Though physiological

differences obviously exist among the three species, the range of tolerance to salinity and osmotic effects is unknown. Characterization of the ecological amplitude of these species and their artificial hybrids may shed light on the importance of edaphic features in the diversification of this group. Other species, especially *L. kunthii* (Less.) Hook and Arn. and *L. glaberrima* DC. (*L.* sect. *Lasthenia*) are also restricted to vernal pools and wetlands, while *L. platycarpha* (A. Gray) Greene [*L.* sect. *Platycarpha* (H. M. Hall) Ornduff] is found predominately in alkali flats (Ornduff 1993).

The survey presented here reveals that the majority of *Lasthenia* species are tolerant of unusual edaphic conditions, and it is reasonable to suggest that these edaphic features have played an important role in the divergence of this relatively small genus. Even within an apparently uniform edaphic habitat, such as a salt flat, populations of different species are rarely sympatric. This strongly suggests that micro-scale differences in edaphic features are likely responsible for their distribution. Although species discussed above are adapted to deal with different specific ions (e.g., heavy metals, magnesium under serpentine, sodium, magnesium under saline, nitrate under guano), an important factor that is common to all these edaphic habitats is the high osmotic pressure of the soil solution. From the information currently available for *Lasthenia* (Ornduff 1965; Rajakaruna and Bohm 1999; Rajakaruna et al. 2003), it appears that ion accumulation and sequestration is a common strategy used to counter this stress. However, there are inter- and intra-specific differences in mechanisms of tolerance to osmotic stress and these differences may have set the stage for the fascinating ecological divergence seen in the genus.

Many *Lasthenia* species occur in land that is geologically rather recent, since a large proportion of their present range was covered by sea water during the Miocene and Pliocene (Howard 1951; Axelrod 1956). The inland sea retreated at the close of the Pliocene, although saltwater lakes of varying extent existed in the Central Valley during the Pleistocene (Flint 1947). Some of the lakes and marshes have persisted into the 19th century (Mason 1957) and it is reasonable to speculate that the ancestor of *Lasthenia* was tolerant of salinity (specific ion effects) and osmotic effects. Salinity and osmotic tolerance may in fact represent ancestral traits that have been retained in the vast majority of species while it has been lost in a few others. Alternately, tolerance to osmotic and salinity effects may have independently evolved in the various species in response to their radiation into unique habitats such as vernal pools, alkali flats, serpentine outcrops, and guano deposits.

The Hawaiian silversword alliance (Asteraceae: Madiinae) provides perhaps the most spectacular and well-studied example of adaptive radiation in plants (Robichaux et al. 1990; Baldwin 1997). The study by Chan et al. (2001) suggests that saltational diversification has also occurred in *Lasthenia,* with a rapid initial radiation, perhaps into distinct ecological niches, followed by long periods of gradual change punctuated by renewed, rapid diversification. *Lasthenia* has no doubt been immensely successful in adapting to the ecological diversity of its present range similar to other Californian genera where catastrophic selection has supposedly operated (Lewis 1962; Vargas et al. 1999).

Edaphically restricted species provide fascinating examples for the study of plant speciation. The study of the processes leading to the evolution of such species can shed light on the relationship between adaptation and speciation. With the advent of genetic techniques such as the study of quantitative trait loci (QTLs), it is possible to study candidate "speciation genes." Perhaps the best-known example in this regard is in the genus *Mimulus* (Bradshaw et al. 1998) where floral traits associated with pollinator preference and reproductive isolation have been characterized. This study implies that genes of large effect can contribute to speciation. A similar association has recently been established in *Aquilegia* (Ranunculaceae) (Hodges et al. 2002). In both these QTL studies, reproductive isolation is a by-product of adaptation to pollinators, thus providing a direct link between adaptation and speciation.

The genus *Lasthenia* provides numerous opportunities to examine the link between adaptation to substrate and reproductive isolation. Many closely related species in *Lasthenia* generally avoid sympatry and appear to be wholly distinct in areas of contact. Thus, these species appear to be both ecologically divergent and reproductively isolated. In *Lasthenia,* the extent of isolation as well as the extent of ecological differentiation among closely related species, has not been well documented except in the case of *L. californica sensu* Ornduff (Rajakaruna and Whitton unpublished). Traits that are associated with ecological specialization in closely related species can be identified and their adaptive significance can be demonstrated. If the ecologically-divergent species are reproductively isolated, it will be possible to examine any links between adaptation to substrate and reproductive isolation, and thus, identify potential "speciation genes."

The available phylogenetic information (Desrochers and Bohm 1995; Chan et al. 2001, 2002; Desrochers and Dodge 2003), along with the relatively small size of the genus, low base chromosome number ($n = 8$), generally annual habit and obligately outcrossing nature, and the ease with which the species can be grown for experimental studies make *Lasthenia* an ideal model for studies in evolutionary ecology.

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ENVIRONMENTAL INFLUENCE ON LEAF GLAUCESCENCE IN WILLOWS (*SALIX*)

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ABSTRACT

Seven native and one naturalized species of *Salix* (Salicaceae) were grown from cuttings in a solar greenhouse to determine the effect of direct sun exposure and shading on leaf glaucescence. All species grown exposed to the sun (except one non-rooting species that died) developed their normal leaf glaucescence. Three of the species that were shaded from the sun developed leaf glaucescence but much less intense than that of the sun exposed plants. The remaining three rooting species of shaded plants did not develop their normal leaf glaucescence until after they were placed in the sun. The shade-produced leaves of one species did not develop glaucescence even after sun exposure although the new leaves that were exposed to the sun did develop glaucescence. Results suggest that leaf glaucescence in *Salix* is only partly genetically controlled and can be modified by environmental factors. Implications of using leaf glauces- cence as a taxonomic characteristic are discussed.

Key Words: Salicaceae, *Salix*, glaucescence, environmental influence.

Leaf glaucescence is the result of a waxy deposit on the surface of the leaf that appears whitish and can be easily rubbed off (Dorn 1977). In the genus *Salix* (Salicaceae), glaucescence is found on the underside of the leaves of some species but not others. It is an important characteristic for identifying many species in this large and difficult genus. It has long been known that using excessive heat to dry specimens can eliminate glaucescence and that some individuals do not display the glaucescence that is characteristic for the species or variety (Raup 1959).

While attempting to root dormant cuttings of *Salix fragilis* L. indoors with no direct sun exposure, I observed that the newly produced leaves did not acquire any glaucescence on their undersides. Leaves are normally glaucous and this characteristic is used, in part, to identify the species. It was uncertain whether the lack of glaucescence was caused by no sun exposure or by the relatively constant room temperature. Accordingly, I selected cuttings of this species and seven additional native species (Table 1) that normally have glaucous leaves to try to determine if temperature or lack of sun exposure was responsible for the lack of glaucescence. The selected species represent two subgenera and six sections in the genus *Salix* (Dorn 1976).

METHODS

Cuttings were collected on 3 January 2002 from seven native species (Table 1) and on 4 January 2002 from *Salix fragilis* being grown in a city park. Cuttings were from the two-year old wood (i.e., growth of two full seasons). The bottom half of the cuttings were placed in untreated well water in individual foam cups on the same day of collection. Three separate cuttings, all from a single plant,

were placed in each cup. All buds were axillary buds. The cups with the cuttings were placed in a solar greenhouse without supplemental heat or light, half of each species shaded from the sun, the other half directly exposed to the sun but immediately adjacent (Fig. 1).

Shading material initially consisted of 2.54 cm thick foam insulation backed with foil. As the sun angle got higher (about seven weeks later on 22 February 2002), this was replaced with a larger sheet of corrugated cardboard. A max/min thermometer was placed among the shaded plants to record temperatures (Table 2). The solar greenhouse faced south and had two layers of glazing separated by 8.9 cm and angled at 60° from horizontal (30° north from vertical). The outer glazing was fiberglass (treated for UV protection ca. 25 years earlier but likely now ineffective), and the inner glazing was polyethylene. The greenhouse was located in Laramie County, Wyoming at 41°09′N 104°54′W, elevation 1890 m. Well water was added to the cups periodically as needed.

Approximately 40–50 days after the cuttings were placed in water, six of the eight species were planted in a potting soil mix in the same cups or additional cups as needed. *Salix bebbiana* and *S. scouleriana* had not rooted. The sun and shade plants continued to be segregated. Voucher specimens were prepared on 4 April 2002 (deposited in RM), and the remaining shade material was all placed in direct sun. Temperatures continued to be recorded in the shade (Table 2). Observations were terminated on 3 May 2002, four months after the start of the experiment. Data recorded for both sun and shade plants included days to (1) first bud break, (2) first root emergence, (3) first root branching, and (4) first detection of leaf glaucescence. Leaf glaucescence was determined by observing

TABLE 1. CLASSIFICATION AND COLLECTION LOCALITIES FOR EIGHT *SALIX* SPECIES IN WYOMING. *Salix amygdaloides* is a lower elevation species, seldom above 2135 m in this area; the remainder (except the non-native *S. fragilis*) are primarily mountain species, mostly above 2135 m. *Salix scouleriana* and to a slight extent *S. bebbiana* are species of drier habitats.

| Subgenus, section, species	Voucher number	County	Latitude/Longitude	Elevation
Subgenus *Salix*				
Section *Humboldtianae*				
S. *amygdaloides* Andersson	9076	Laramie	41°10′N 104°53′W	1890 m
Section *Salix*				
S. *fragilis* L.	9071	Laramie	41°10′N 104°50′W	1860 m
Subgenus *Vetrix*				
Section *Glaucae*				
S. *brachycarpa* Nutt.	9075	Albany	41°13′N 105°20′W	2410 m
Section *Cinerella*				
S. *bebbiana* Sarg.	died	Albany	41°13′N 105°20′W	2410 m
S. *scouleriana* Barratt ex Hook.	9077	Albany	41°14′N 105°23′W	2560 m
Section *Viminella*				
S. *planifolia* Pursh	9074	Albany	41°13′N 105°20′W	2410 m
Section *Cordatae*				
S. *eriocephala* Michx. var. *ligulifolia* (C. R. Ball) Dorn	9073	Laramie	41°10′N 104°53′W	1890 m
S. *monticola* Bebb	9072	Albany	41°14′N 105°22′W	2500 m

1 meter
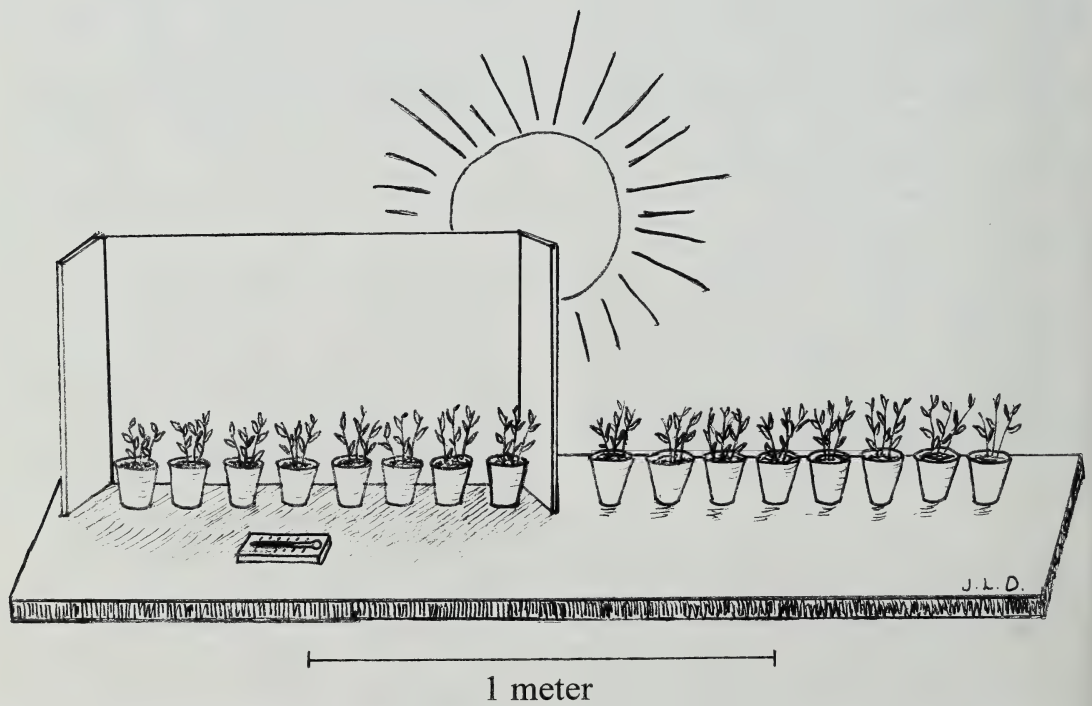
FIG. 1. Sketch of experimental arrangement to test the effect of direct sun exposure and shading on leaf glaucescence.

TABLE 2. SUMMARY OF GREENHOUSE SHADE TEMPERATURES AT THE LEVEL OF EXPERIMENTAL WILLOW PLANTS, INCLUDING OUTSIDE CLOUD COVER DATA. Temperature data were recorded daily at 7:30 a.m. for the previous 24-hour period.

	Temperature (°C)				Number of days with 100% cloud cover for all daylight hours
	High		Low		
Month	Absolute	Average	Absolute	Average	
January, 2002	33.9	27.3	5.0	8.9	2
February, 2002	33.9	28.8	5.6	10.4	0
March, 2002	32.2	26.6	6.7	11.4	3
April, 2002	36.1	28.6	8.9	14.2	4

the whitish color and confirmed by rubbing off a portion with a finger on the living plants.

RESULTS

Two of the species, *Salix bebbiana* and *S. scouleriana,* did not produce roots. *Salix bebbiana* did not produce leaves large enough to detect possible glaucescence and appeared dead after about 65 days. *Salix scouleriana* produced leaves about one-third their average expanded size before growth stopped after about 50 days. The plants exposed to the sun showed slight leaf glaucescence and the shaded plants did not show any leaf glaucescence (Table 3).

Days to first bud break ranged from 10 or 11 days for two mountain species, *Salix brachycarpa* and *S. planifolia,* to 32 days for a lowland species, *S. amygdaloides.* There was little difference between sun exposed and shaded plants of the same species (Table 3). Days to first root emergence and first root branching showed only minor differences from species to species and from sun exposed to shaded plants except for *S. brachycarpa* which had delayed root branching in shaded plants (Table 3).

None of the youngest leaves showed any glaucescence. It took from 11 to 33 days after bud break for glaucescence to be detectable in sun-exposed plants and 18 to 69 days in shaded plants.

The shaded plants that had glaucescence had very faint glaucescence, initially. Glaucescence slowly increased in intensity with time but never

reached the intensity of the sun-exposed plants. The three shaded species that did not show any glaucescence after 90 days (*Salix amygdaloides, S. fragilis, S. planifolia*) took from 3 to 23 days after being placed in the sun to show glaucescence. In the case of *S. fragilis,* only the new leaves showed glaucescence, and the old shade-produced leaves remained non-glaucous.

DISCUSSION

This experiment suggests that leaf glaucescence in willows is only partly genetically controlled and can be modified by environmental factors. This has been noted in other plant families including Myrtaceae, Fabaceae, and Brassicaceae (Metcalfe and Chalk 1979; Baker 1982). Metcalfe and Chalk (1979) postulated that glaucescence reflects light so that glaucous leaves would be disadvantageous in shaded environments. In the case of willows, species with glaucous leaves and species with non-glaucous leaves frequently grow side by side in full sun, and neither group does well in shaded situations. This hypothesis appears to be irrelevant in the case of willows.

If shaded conditions inhibit the manifestation of leaf glaucescence in some willow species, what significance might this have on species identifications when leaf glaucescence or lack thereof is a primary identification characteristic? There are only six species or varietal pairs of North American willows that are distinguished primarily or exclusively by glau-

TABLE 3. OBSERVATIONS FOR EIGHT *SALIX* SPECIES GROWN IN SUN AND SHADE. [a] After being placed in direct sun following 90 days in shade. [b] (—) indicates that this species did not root or produce large enough leaves to develop glaucescence.

Species	Days to bud break		Days to root emergence		Days to root branching		Days to glaucescence	
	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade
S. amygdaloides	30	32	31	30	39	40	49	17[a]
S. fragilis	26	21	19	17	31	31	45	23[a]
S. brachycarpa	10	10	22	22	33	45	43	79
S. bebbiana	19	19	—[b]	—[b]	—[b]	—[b]	—[b]	—[b]
S. scouleriana	18	18	—[b]	—[b]	—[b]	—[b]	44	—[b]
S. planifolia	11	10	26	27	35	36	31	3[a]
S. eriocephala var. ligulifolia	18	18	20	20	31	34	31	46
S. monticola	23	23	22	22	33	35	34	41

cous versus non-glaucous leaves: *Salix nigra* Marshall—*S. caroliniana* Michx., *S. lucida* Muhl.—*S. lasiandra* Benth., *S. lasiandra* var. *lasiandra*—var. *caudata* (Nutt.) Sudw., *S. eriocephala* Michx. var. *mackenzieana* (Hook.) Dorn—var. *monochroma* (C. R. Ball) Dorn, *S. eriocephala*—*S. cordata* Michx., *S. myrtillifolia* Andersson—*S. ballii* Dorn. Where intergrading has been suspected or documented, it has usually been interpreted as the result of hybridization (Argus 1986a; Dorn 1995). It is unknown how many misidentifications occur due to normally glaucous-leaved species or varieties lacking glaucescence.

Based on field observations, the biggest potential for misinterpretation appears to be with the *Salix lucida*—*S. lasiandra* complex and with *S. eriocephala* var. *mackenzieana*—var. *monochroma*. Although the latter pair has not been examined in detail, they were found growing at the same location in several areas, and in one case, the glaucous leaves of var. *mackenzieana* lost their glaucescence in drying (Dorn 1995). Argus (1986b) sampled over 800 specimens in the *S. lucida*—*S. lasiandra* complex and found that all specimens assigned to *S. lucida* and *S. lasiandra* var. *caudata* had non-glaucous leaves while *S. lasiandra* var. *lasiandra* specimens were 88% glaucous and 12% non-glaucous. In addition, *S. lucida* specimens were 71% hypostamatous, *S. lasiandra* var. *lasiandra* 67% hypostomatous, and *S. lasiandra* var. *caudata* 6% hypostomatous. If all specimens were assigned to the correct taxon, then the 12% of *S. lasiandra* var. *lasiandra* specimens that had non-glaucous leaves would be the only problem specimens. *Salix lucida* and *S. lasiandra* var. *caudata* have non-glaucous leaves and are allopatric so they should not be confused.

The range of *Salix lasiandra* var. *lasiandra* overlaps with both of the other taxa. It is in these overlap areas where environmentally influenced specimens of *S. lasiandra* var. *lasiandra* might be incorrectly identified if the leaves are non-glaucous, although this is not especially critical for the varieties of *S. lasiandra*. It becomes critical in the case of *S. lucida* and *S. lasiandra* var. *lasiandra* because the glaucescence variability in var. *lasiandra,* the stomata variability in both, and variability in other

vegetative characteristics prompted Argus (1986b) to subordinate both varieties of *S. lasiandra* as subspecies of *S. lucida* even though he pointed out that, "I have not seen populations that contain both taxa . . ." (referring to *S. lucida* and var. *lasiandra*). Cuttings of *S. lasiandra* var. *lasiandra* from a range overlap area in Saskatchewan were grown in an experimental garden by Argus (1986b), and he found that the leaf glaucescence evident in the field was not exhibited in the garden. Could his specimens "that seem to be intermediates" have been responding to environmental conditions rather than hybridizing? This remains an open question.

Leaf glaucescence is a useful characteristic for identifying species of *Salix*. Lack of glaucescence in normally glaucous-leaved taxa needs to be used cautiously when it is the basis for taxonomic realignments. This is one more example of the morphological plasticity in most species of willows.

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WINTER EPHEMERAL VEGETATION AND SEED BANKS OF FOUR NORTH-FACING SLOPES IN THE SONORAN DESERT

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ABSTRACT

Variable temperature and precipitation in hot deserts interact to trigger germination of ephemeral plants; however, in the Sonoran Desert, little information is available on how these winter ephemeral plant communities vary among localities and how the seed bank contributes to the above ground diversity. This study quantifies the similarity in seed banks (below ground flora) of winter ephemeral plants among sites and the relationship to the above ground flora. In November 1999, ninety-five soil samples were collected across four Sonoran Desert localities and germinated in a glass house under site temperature and light conditions and were misted daily. In February 2001, when winter rains were sufficient to germinate winter ephemerals *in situ,* the same four localities were revisited and data were taken on the genera present within plots. The Jaccard Similarity Index, Margalef Diversity Index, lists of taxa, and densities of common taxa were compared among sites and between the seed bank and above ground flora. Overall, seed bank similarity of taxa among sites averaged 41% whereas the above and below ground data averaged 49% similarity. Only three of 36 genera were present in the seed bank and above ground flora in all sites: *Pectocarya* DC. ex Meisn.(Boraginaceae), *Eucrypta* Nutt. (Hydrophyllaceae), and *Amsinckia* Lehm. (Boraginaceae); the density of these varied significantly among sites and between above and below ground floras. The Poaceae taxa, *Poa bigelovii* Vasey & Scribn., *Vulpia octoflora* (Walter) Rydb., *Schismus arabicus* Nees, and *Bromus rubens* L., were notably dominant in the seed bank while less dense in the above ground flora. Due to the variability of seed banks and above ground floras, adding seed bank analysis to the above ground vegetation data taken in most studies would enhance our understanding of overall site diversity.

Key Words: Winter ephemerals, seed bank, above ground vegetation, Sonoran.

Desert winter ephemeral plant communities are highly structured by fluctuations in precipitation and temperature (Went 1948; Sala and Lauenroth 1982; Venable and Pake 1999). In fact, the interplay between these two factors drives temporal variation of ephemeral plant diversity in the Mojave Desert (Beatley 1974) with specific temperatures and precipitation combinations resulting not only in different winter and summer vegetation, but in different species dominating between winters and between summers (Tevis 1958a, b). Likewise, geographic variability of germination within the same season has been documented for several populations in the Mojave and Sonoran Deserts (Shreve 1951; Epling et al. 1960; Pake and Venable 1996), and other studies have commented on these differences between years (Roberts 1986; Coffin and Lauenroth 1989). Ephemeral plants are here defined as those plants germinating in response to unpredictable seasonal precipitation and temperature cues; they are not considered to be annuals since several years may pass before germination occurs.

Few large scale comparisons have been made among the four North American deserts (Guo et al. 1998, 1999) with most studies having focused on single sites within the same desert (Went 1948; Burk 1982). These studies have examined seed bank dynamics by studying seed distribution, species composition (Tevis 1958a, b; Bowers 1987; Henderson et al. 1988), and germination conditions (Harlan and Went 1945; Juhren et al. 1956). Seed bank dynamics play a large role in maintaining ephemeral plant diversity in arid areas. Not only do they increase the ability for species to persist in arid environments (Epling et al. 1960), but by germinating less than 100% of its seeds each season (Baskin and Baskin 1978), depletion of the seed bank in a given area is unlikely (Venable and Lawlor 1980). Diversity is thus actually greater per unit area since many species are able to coexist in germinated and ungerminated conditions and not simultaneously compete for resources (Pake and Venable 1996).

Shreve (1951) was the first to note the drastic changes in diversity that can occur in a Sonoran Desert winter ephemeral plant community when heavy rains elicit germination of rarer species. These regional germination events are often linked to the El Niño climate cycle which brings above average winter rainfall to the desert when critical temperatures break seed dormancy (Venable and Pake 1999); more often, off-El Niño rainfall triggers localized flowering events every three to four years (Dimmitt 2000; but see Jennings 2001). For

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these smaller, isolated blooms, taxonomic similarity or the contribution of the seed bank has been little explored in the Sonoran Desert. Multi-site seed bank and above ground flora studies are lacking although some anecdotal evidence exists for floristic dissimilarities between proximal sites. For example, Went (1948) noted that in adjacent areas in the Mojave Desert, different populations of ephemeral species existed. In a Chihuahuan Desert study, sites separated by as little as four km differed significantly in plant density and species diversity (Dye 1969, cited in Kemp 1989). By investigating the geographic heterogeneity of ephemeral plant germination as well as the contribution of the seed bank to the above ground flora, a better understanding of Sonoran Desert seed bank dynamics and ephemeral diversity is gained and differences among North American Deserts can be further explored. This study compares the floristic similarity of winter ephemeral plants among four localities and analyzes the contribution of the seed bank to the above ground flora. Data from seed bank and field studies from four Sonoran Desert sites in the Phoenix area are used to make these comparisons.

METHODS

Study sites. The city of Phoenix, Arizona has preserved 33% of its land in the form of desert mountain preserves (Morrison Institute 2000). All four study sites are located in desert remnants in the metropolitan Phoenix area under the jurisdiction of Phoenix City Parks or the U.S. Military (Fig. 1). All of these areas are relatively undisturbed and are characterized as Sonoran Desert Scrub (Brown and Lowe 1994) and are dominated by *Larrea tridentata* (Sesse & Moc. ex DC.) Coville (Zygophyllaceae), *Parkinsonia microphylla* Torr. (Fabaceae), and *Ambrosia deltoidea* (Torr.) W.W. Payne (Asteraceae). To be consistent in microclimate, north-facing slopes were chosen for all sites. Sites were selected based on winter ephemeral diversity as observed personally or reported by park rangers and local botanists. North Barnes Butte, which was believed to be species poor based on previous fieldwork, was added for comparison since the data was to be collected for another simultaneous project.

The North Barnes Butte (BB) site is located on the Arizona National Guard Papago Park Military Reservation at 33°27'N; 111°57'W. The 157 ha base is bordered on all sides by residential areas and has been fenced since 1909 keeping the area relatively undisturbed. Historical site activity include the foundation of a homestead (ca. 1800's) and probable usage by the Maricopa and Pima peoples (Gart 1996). While military exercises are carried out to the north of the butte, the butte itself is rarely used since it flanks an active firing range. Soil analyses showed that the area is a sandy loam with an average pH of 6.6, organic matter 2.9% and nitrate 23 ppm.

The Shaw Butte (SB) site is located in the North Mountain Recreation Area of the 7000 ha Phoenix Mountains Preserve at 33°35'N and 112°4'W. This site is located near the edge of the preserve, though not adjacent to any designated trail. Soil for this area is loam with a pH of 7.0, 2.7% organic matter, and nitrate 16.5 ppm.

The South Mountain (SM) site is located in South Mountain Park at 33°15'N and 112°5'W. South Mountain Park became a 16,677 ha city park in 1924. The study site was located over a mile from hiking trails, though within site of a residential area. Previous usage of the area includes an abandoned home site (pre-1950's) visible from the collection area. The soil is a sandy loam with a pH of 6.9, 1.9% organic matter, and nitrate 18 ppm.

The Squaw Peak (SQ) site is located in the Squaw Peak Recreation Area in the Phoenix Mountains Preserve at 33°31'N and 112°1'W. The entire Preserve spans 2833 ha and was created in the 1960's with the Squaw Peak portion first set aside in 1910. Verbal reports of previous mining and grazing activities exist for the general area, but not specifically for the study site. Soil at this site is characterized as loam with a pH of 6.05, 2.15% organic matter and 12 ppm nitrate.

Seed bank sampling. Soil samples were collected October–December 1999 for soil seed bank germination. Soil was sampled from open areas adjacent to *Parkinsonia microphylla* or *Ferocactus cylindraceus* (Engelm.) Orcutt (Cactaceae) plants at each site, which are widely dispersed across the slopes. Ninety-five total samples were collected, 20–25 samples per site, using a 6.4 cm diameter copper cylinder that was pressed 2 cm into the soil—the average depth of the active soil seed bank (Childs and Goodall 1973). To account for heterogeneity of seed distribution in the soil (Nelson and Chew 1977; Bertiller and Coronato 1994), each of the 20–25 soil samples (128.7 cm³ per sample) was composed of four pooled sub-samples (Bigwood and Inouye 1988). Across all samples at each site, a surface area of 0.3 m² was studied.

Since seeds do not germinate when they are buried greater than 1 cm below the ground (Freas and Kemp 1983), 103 cm³ of each field soil sample (80%) was spread 1 cm deep over an autoclaved mixture of potting soil and pumice in each of two (10 × 10 cm) pots. These were placed in a randomized block design in a non-heated, evaporatively cooled greenhouse. Trays of the autoclaved soil and pumice mixture were interspersed with the collected soil samples to detect sample cross contamination. Samples were misted with water once a day to maximize germination and to avoid desiccation. Temperatures inside the greenhouse fluctuated like those at the study sites, though being slightly higher or lower on occasion, but met the seasonal germination requirements of most winter ephemerals (Baskin and Baskin 1998). All plants, including any
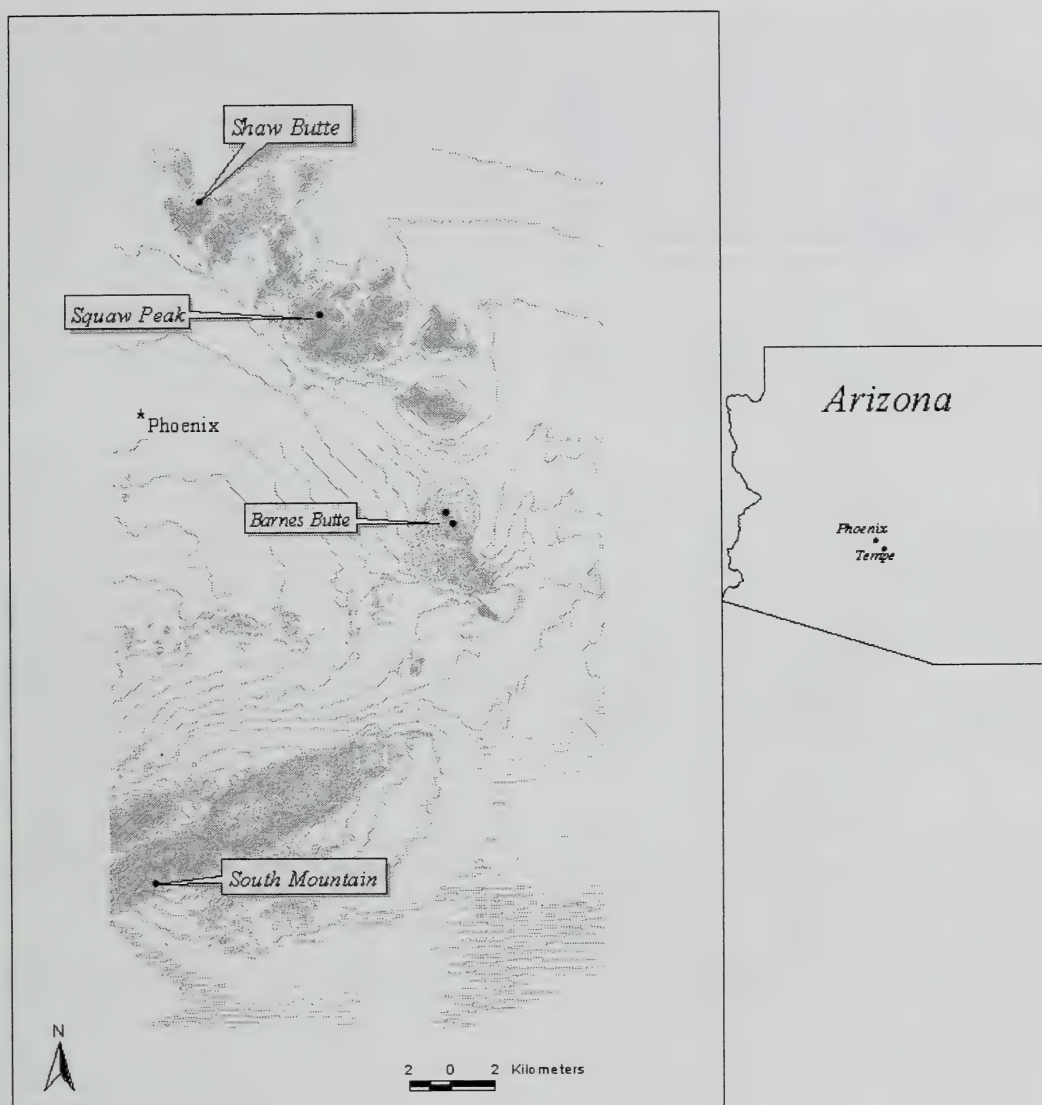
FIG. 1.   Study areas located in the Metropolitan Phoenix area, Arizona.

perennials and grasses, were inventoried weekly from October 1999–March 2000. All taxa were identified to species when possible (some died before flowering) and vouchered at the ASU herbarium with nomenclature following the USDA National Plants Database (2001). To convert greenhouse densities of plants to densities expected in the field, all greenhouse plant densities were divided by 80%, which was the amount of field soil germinated in the greenhouse.

Field sampling. Sufficient rain fell in the winter of 2000–2001 for successful in situ germination of winter ephemeral plants. Thus, in February 2001, the same areas where soil samples were taken for the seed bank study were revisited. The same or

adjacent trees were resampled with fifteen 2 × 2 dm vegetative plots each located two paces down slope from each tree. For each plot, the number of individuals per genus were recorded. For each study site, 0.6 m^2 was sampled.

Climatic measurements. In 1999–2000, Greenhouse temperatures were monitored every two days for high and low temperatures. These were compared with outside greenhouse temperatures also monitored on site to ensure that the greenhouse was within range of normal outside temperatures. Monthly field temperatures and precipitation for 2000 were secured from the National Weather Service in Phoenix, Arizona (National Weather Service 2001).
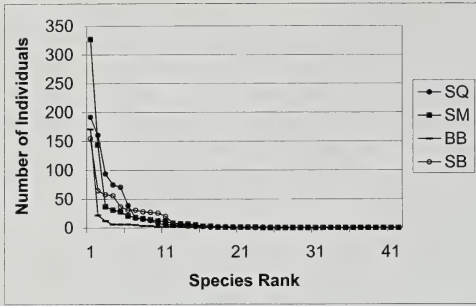
FIG. 2. Rank abundance curves for four sites showing that most sites were characterized by a few dominants and numerous rare species.

TABLE 1. DIFFERENCES IN NUMBERS OF SPECIES (S), THE MARGALEF INDEX (D_{Mg}) AND DENSITY AMONG STUDY SITES. Higher Margalef scores indicate higher diversity and density.

	S	D_{Mg}	Density individuals/m²
N. Barnes Butte (BB)	19	3.26	820.4
Shaw Butte (SB)	26	3.94	1392.8
South Mountain (SM)	23	3.36	1949.6
Squaw Peak (SQ)	22	3.20	2102.3

Statistics and indices. The following indices and measures were calculated: number of taxa, density, the Margalef index (Magurran 1988), Jaccard Similarity Index (Magurran 1988), average density and average diversity per unit area. These were chosen because they are common measures in other studies; in addition, the Margalef combines density and diversity into a single number that facilitates comparisons between data sets. Higher scores indicate higher diversity. The Margalef was calculated as follows:

$$D_{Mg} = \frac{(S - 1)}{\ln N}$$

where S equals the number of taxa recorded and N is the number of individuals summed over all taxa in the sample. ANOVAs were conducted on square-root transformed Margalef Index scores of the seed bank data. Scheffé tests were applied to determine significant differences in diversity among sites.

To compare changes in taxa that were dominant at all sites, the seed bank data were used. Due to the many zeros in the data set, averages of plants/sample were compared with the Wilcoxon (W) test in SAS 8.1 (2000). For comparison of the above and below ground floras for the most common genera, both data from the greenhouse (below ground/seed bank) and the field (above ground) were used. Genera were used due to a plant identification error of the two *Amsinckia* species in the seed bank study; therefore all *Amsinckia* determinations were lumped into the genus. Because these methods used different plot dimensions, all numbers were converted to individuals per square decimeter before conducting Wilcoxon tests. Ancillary graphs were created using Microsoft Excel 2000.

Rank abundance curves were calculated for each site by ordering all taxa per site from most to least abundant (based on number of individuals) and then plotting them in that order versus the number of individuals for that taxa. This allows one to examine the distribution of taxa as being predominantly rare or common for a given area. For ex-

ample, *Pectocarya* was ranked first at SM, numbering nearly 350 individuals (see Fig. 2).

RESULTS

Among site comparisons of below ground flora. Based on seed bank data alone, there were 34 winter ephemeral genera and 43 species (Appendix A). *Crassula erecta* (Hook. & Arn.) A. Berger (Crassulaceae) was excluded from the analysis due to its prolific seed production, self sowing, and re-germination that would have augmented seedling counts. Sites ranged from 19–26 species with an average of 22.5 species per site. Densities ranged from 820–2102 individuals/m² (Table 1).

Sixteen of these taxa (37%) were found at only one site; 10 taxa (23%) were common to two sites; 10 taxa (23%) were common to three sites; and only six taxa (14%) were found at all four sites, namely *Schismus arabicus, Pectocarya recurvata* I.M. Johnst., *Amsinckia* spp., *Poa bigelovii, Vulpia octoflora*, and *Eucrypta micrantha* (Torr.) A. Heller. Most taxa were rare in occurrence with only a few, such as the above, being numerous (Fig. 2). Using the Margalef index to indicate highest diversity across sites, all sites were similar in species richness with only Barnes Butte and Shaw Butte being significantly different ($F_{3,.05} = 3.87$, P = 0.0117) (Fig. 3). Generic Jaccard similarity indices among sites averaged 41%. SB and BB were the least similar in composition with 24% similarity of species richness whereas BB and SQ received the highest Jaccard Similarity Index of 58%. Other sites fell in
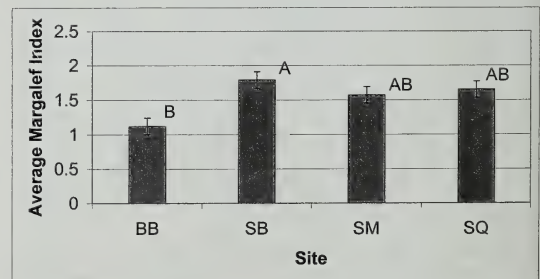

FIG. 3. Average Margalef diversity index scores of seed banks. Sites with different letters are significantly different and higher scores indicate higher diversity.
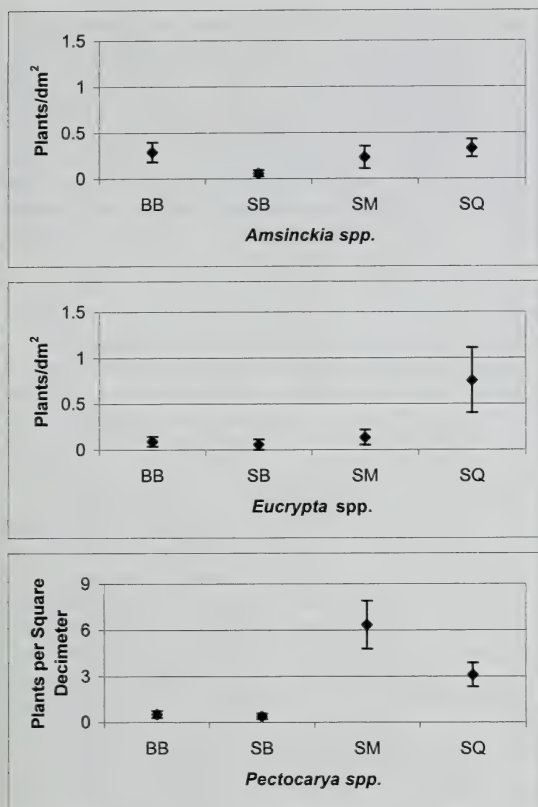
FIG. 4. A comparison of taxa density among the seed banks of the four study sites. Note scale change for *Pectocarya*. Bars denote standard error.

amined for density among sites, not all species were represented equally; furthermore, half of these dominants were grasses, including the naturalized exotic, *Schismus*. When *Eucrypta* density was examined, there was a significant difference among sites ($W_{3.05}$ = 16.4022, P = 0.0009); *Pectocarya* exhibited the same trend ($W_{3.05}$ = 37.3922, P < 0.0001). However, for *Amsinckia* ($W_{3.05}$ = 6.6909, P = 0.0824), there was no significant difference in density among sites (Fig. 4).

Below ground and above ground comparisons. When the data for the seed bank and above ground flora studies were combined at the generic level, 36 genera were present at all sites. There was an average 49% taxonomic similarity between above and below ground floras with SQ having 46% similarity, SB with 48%, and both BB and SM having a 50% similarity between above and below ground floras at those sites. Three grass species were dominant in all sites in the seed bank, though scarcely present in the above ground flora. However, despite the changes in the presence or absence of rarer plants, three genera were always present at all sites in the seed bank and the above ground flora, although not always in the same proportions. *Eucrypta* was significantly denser in the field ($W_{3.05}$ = 5571, P < 0.0003); however, *Pectocarya* ($W_{3.05}$ = 4835.5, P = 0.56) and *Amsinckia* ($W_{3.05}$ = 4488, P = 0.36) were not (Fig. 5).

Temperature and precipitation comparison between field and greenhouse. Greenhouse temperatures were 5–19°F higher in the day and 4–8°F cooler at night thus potentially allowing for more germination cues to be met. Greenhouse plants were misted for 10 minutes per day while Phoenix sites received 0–3.17 inches of rain per month. Seed bank germination occurred primarily during the first two weeks of irrigation with limited germination thereafter.

between these ranges with SM having 34% of its species in common with BB and 48% similarity with SB. SQ was least similar to SM (39%) and next most similar to SB (41%).
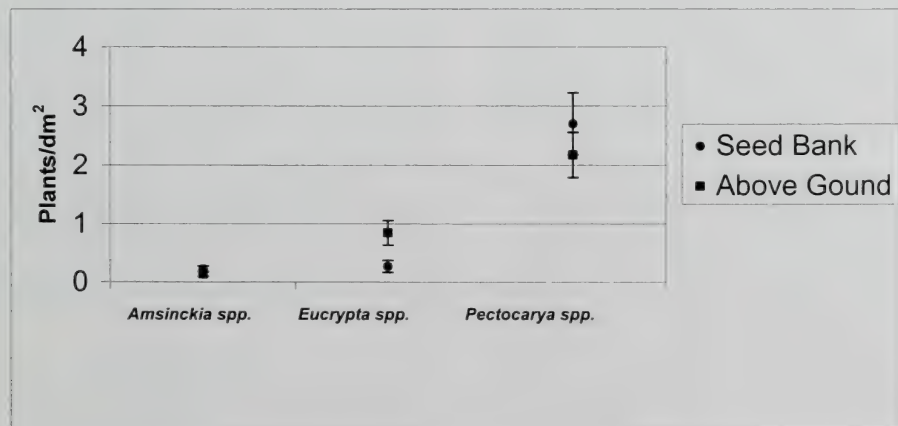
When the six taxa common to all sites were ex-

FIG. 5. A comparison of the density of the three genera common in both the above and below ground floras. Bars denote standard error.

DISCUSSION

Quantities of light and water determine which areas are suitable for germination in a particular season. This combination is never the same: as each species varies slightly in its germination requirements, the mix of germinating species in a locality can change from year to year (Grubb 1977). For example, in Went's early studies of *Pectocarya, Plantago* L. (Plantaginaceae), and *Schismus,* different precipitation and temperature conditions resulted in domination of different taxa (Went 1948, 1949). In my Sonoran Desert study sites, there was a 49% taxonomic similarity between the above and below ground floras despite differences in dominants and rarer taxa. In keeping with Shreve's observations of changes in dominant taxa between years, although *Eucrypta* accounted for approximately 40% of all individuals at SB in the above ground vegetation, below ground it accounted for only 5%. Similarly, in a six-year Mojave Desert field study, 34 of the 62 study species occurred every year and only eight occurred in a single year (Bowers 1987). However, not all taxa shifted drastically in dominance above and below ground. At SM, for instance, *Pectocarya* was dominant in both above and below ground floras. Grasses, however, had the greatest response, with *Poa, Schismus,* and *Vulpia* dominating the seed bank but not the above ground flora.

The change in dominance of grasses between the seed bank and the above ground flora yields evidence of the environmental triggers for the germination of this guild. The difference probably lies in the greater water availability in the greenhouse while the field received only 16 cm of rain. *Schismus* responds well to high water availability (Szarek et al. 1982) often outranking *Plantago* in mesic conditions; however, *Bromus rubens,* another exotic grass, dominated the seed bank of SQ but was absent in the above ground flora despite dominating local riparian areas that same spring (Boudell personal communication). Nonetheless, grasses can change from rare to common in the above ground flora as evidenced by the Chihuahuan Desert study where the density of *Vulpia octoflora* significantly increased over the course of 15 years (Guo et al. 2000).

Species dominance also varies among localities in the seed bank. Among the seed bank floras of the four sites, there was a 41% overlap among taxa with most taxa being represented by few individuals. There was less similarity among seed banks than between each sites seed bank and above ground flora. Of the 42 species, 38% were only found in a single site and only 14% were found at all sites. Likewise in a desert grassland study 21 of the 45 were species restricted to less than five percent of all samples (Henderson et al. 1988). These results suggest that there is a different plant assemblage and high turnover at each location despite similar aspect, soil, and woody vegetation.

In this study, only six taxa were common to all sites. Of these, I evaluated the three non-Poaceae taxa. These were the only genera common at all sites in both the seed bank and above ground flora, although their densities varied. Only *Eucrypta* was significantly different between above and below ground floras while *Pectocarya* and *Amsinckia* were not. These common desert plants, while fluctuating themselves, are surrounded by many other taxa that appear and disappear from the above ground flora while remaining in the seed bank.

Data from this study are based on field-sampled quadrats and greenhouse-germinated soil samples that potentially underestimate plant diversity: two years of data are not enough to fully comprehend the temporal variability of these winter ephemeral assemblages. Above ground data were based on one month's study not allowing for plants blooming outside of that window to be included (see Jennings 2001). When compared to the below ground data, six months of continuous monitoring, as well as a wider range of temperatures, potentially allowed for more taxa to be represented in the seed bank. Furthermore, the above data were collected 14 months after the soil samples when winter rains were next sufficient to induce germination; the interim months may have allowed granivory to occur (Price and Reichman 1987). However, whether one compares methods or years, the conclusion is still the same: different environmental conditions result in the germination of different taxa contributing to the variability between above ground and seed bank floras.

The combination of species with different germination requirements promotes species coexistence within a small scale (Pake and Venable 1996). However, this study suggests that plants also coexist on a larger scale. Variable weather patterns coupled with unique dormancy requirements and limited dispersal creates a potential mosaic of winter ephemeral diversity that varies greatly from area to area as well as above and below ground. This influences our concepts of rarity and commonness, which in the desert take on a spatial and temporal component: what may be locally rare one year might be very abundant the following year. The diversity stored in the seed bank is not often considered in the formation of these concepts. If both dormant and germinated seeds were used to characterize the plant species diversity of an area, it is possible that taxa that were once thought to be rare may actually be quite common, awaiting a temporal germination niche seasonally and unpredictably realized.

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APPENDIX A.   WINTER EPHEMERAL PLANT SPECIES GERMINATED DURING SEED BANK STUDY.

		Site			
Taxon	Family	BB	SB	SM	SQ
Amsinckia spp.	Boraginaceae	x	x	x	x
Astragalus nuttallianus DC.	Fabaceae		x	x	
Bowlesia incana Ruiz & Pav.	Apiaceae	x		x	x
Bromus carinatus Hook. & Arn.	Poaceae		x		
Bromus rubens L.	Poaceae		x	x	
Calandrinia ciliata (Ruiz & Pav.) DC.	Portulacaceae		x		
Calycoseris wrightii A. Gray	Asteraceae			x	
Camissonia californica (Nutt. ex Torr. & A. Gray) P.H. Raven	Onagraceae		x		
Caulanthus lasiophyllus (Hook. & Arn.) Payson	Brassicaceae				x
Crassula erecta (Hook. & Arn.) A. Berger	Crassulaceae	x	x	x	x
Cryptantha barbigera (A. Gray) Greene	Boraginaceae		x		
Cryptantha decipiens (M.E. Jones) A. Heller	Boraginaceae	x			
Cryptantha maritima (Greene) Greene	Boraginaceae	x	x		x
Cryptantha pterocarya (Torr.) Greene	Boraginaceae			x	
Daucus pusillus Michx.	Apiaceae		x		
Dichelostemma pulchellum (Salisb.) A. Heller	Liliaceae			x	
Draba cuneifolia Nutt. ex Torr. & A. Gray	Brassicaceae	x		x	x
Erodium cicutarium (L.) L'Her. ex Aiton	Geraniaceae		x		x
Eschscholzia californica Cham.	Papaveraceae		x	x	x
Eucrypta micrantha (Torr.) A. Heller	Hydrophyllaceae	x	x	x	x
Filago arizonica A. Gray	Asteraceae	x		x	x
Gilia Ruiz & Pav. sp.	Polemoniaceae				x
Lepidium lasiocarpum Nutt. ex Torr. & A. Gray	Brassicaceae		x	x	x
Lesquerella gordonii (A. Gray) S. Watson	Brassicaceae		x		
Linanthus Benth. sp.	Polemoniaceae		x	x	
Lotus sp.	Fabaceae		x	x	
Lupinus sparsiflorus Benth.	Fabaceae		x	x	
Monolepis nuttalliana (Schult.) Greene	Chenopodiaceae	x			
Muhlenbergia microsperma (DC.) Kunth	Poaceae		x		x
Parietaria hespera B.D. Hinton	Urticaceae	x			x
Pectocarya heterocarpa (I.M. Johnst.) I.M. Johnst.	Boraginaceae			x	
Pectocarya platycarpa (Munz & I.M. Johnst.) Munz & I.M. Johnst.	Boraginaceae	x		x	x
Pectocarya recurvata I.M. Johnst.	Boraginaceae	x	x	x	x
Perityle emoryi Torr.	Asteraceae	x		x	
Phacelia distans Benth.	Hydrophyllaceae	x	x		x
Plagiobothrys arizonicus (A. Gray) Greene ex A. Gray	Boraginaceae			x	
Plantago ovata Forssk.	Plantaginaceae	x	x	x	
Plantago patagonica Jacq.	Plantaginaceae	x	x		x
Poa bigelovii Vasey & Scribn.	Poaceae	x	x	x	x
Schismus arabicus Nees.	Poaceae	x	x	x	x
Silene antirrhina L.	Caryophyllaceae		x		
Sisymbrium irio L.	Brassicaceae				x
Vulpia octoflora (Walt.) Rydb.	Poaceae	x	x	x	x

NOTEWORTHY COLLECTIONS

ARIZONA

ERIOGONUM ERICIFOLIUM Torr. & A. Gray (POLYGON-ACEAE).—Pima Co., approximately 43 km SE of downtown Tucson and about 1.8 km W of Cross Hill near the old Pantano railroad siding, and 0.3 km S of Marsh Station Road (mapped as Pantano Road on USGS Rincon Peak 7.5′ Quad.) near an inactive claypit, and about 1 km N of the Southern Pacific Railroad tracks and Cienega Creek where local and scattered on arid, sparsely vegetated low rolling clay hills within Pantano Formation, Claystone Member Deposits with some gypsum evident on the surface in desertscrub and desert grassland in association with *Larrea divaricata*, *Tiquilia canescens*, *Acacia* spp., and *Erioneuron pulchellum*, T16S, R17E, sect. 27 NE¼ of SE¼, 32°00′37.0″N; 110°35′57.6″W, 1082 m elevation, 7 Nov 2002, *R. Duncan s.n.* (ARIZ, NY, US).

Previous knowledge. Until recently there are three recognized varieties of *Eriogonum ericifolium* (Reveal, J.L. & J. Henrickson, Madroño 23:205–209. 1975) with each widely disjunct, two in Arizona (var. *ericifolium*: Yavapai Co, Verde Valley; var. *pulchrum* (Eastw.) Reveal: Coconino Co., Meteor Crater and vicinity near Winslow) and one in California (var. *thornei* Reveal & Henrickson: San Bernardino Co., New York Mountains). Recently L. M. Shultz (Harvard Pap. Bot. 3:51. 1998) elevated the latter to species status and given her rationale it would be reasonable to re-establish *E. pulchrum*. Until now, Arizona populations of *E. ericifolium* were limited to Tertiary gypsophyllous limestone lakebed deposits (Verde Valley) and sandstone. Both *E. pulchrum* and *E. thornei* occur on substrates derived from quartzite and limestone respectively.

Significance. This collection represents the first record of this species from Pima County and is the most southerly locality in Arizona, which is a 282 km range gap between the nearest other population in Yavapai County. Land ownership associated with this new *E. ericifolium* population is mostly Arizona State Trust and to a lesser extent Pima County and private. Due to the rareness of this species in Pima County, land management agencies should be aware of the potential impacts that could result from various activities including clay mining, urban development, off-road vehicle use, livestock grazing/trampling, construction of roads and utility corridors, and recreational developments. Conservation measures are recommended, including consideration for protection under Arizona Native Plant Law as administered by Arizona Department of Agriculture.

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CALIFORNIA

PINUS LAMBERTIANA Douglas (PINACEAE).—San Diego Co., Palomar Mountain, near summit "5696" on the Boucher Peak USGS 7.5 minute topographic quadrangle, 0.5 km NW of the Fry Creek campground, 33°21′02″N, 116°53′26″W, ca. 1700 m, 21 Aug 2002, *Goforth & Minnich s.m.* (UCR).

Previous knowledge. Extensive field mapping across the southern California Peninsular ranges in the Vegetation Type Map (VTM) survey (Griffin and Critchfield 1976, Research Paper PSW-82, U.S. Forest Service) and subsequent aerial photographic surveys (Minnich and Everett 2001, Madroño 49:177–197) recorded *P. lambertiana* on the San Jacinto Mountains, Hot Springs Mountain, and on the Cuyamaca Mountains. *P. lambertiana* was not known to occur on Palomar Mountain (Beauchamp 1986, A flora of San Diego County, California, Sweetwater River Press).

Significance. This is the first collection of *P. lambertiana* from Palomar Mountain. The nearest stands in the Peninsular range occur on the summits of Hot Springs Mountain (29 km E), Thomas Mountain (35 km NE), Santa Rosa Mountain (43 km NE), and North Peak of the Cuyamaca Mountains (46 km SE, Minnich and Everett 2001, *loc. cit.*). Intervening basins and mountains that separate these widely disjunct stands are covered by southern oak woodland, chaparral, and exotic annual grassland.

Three large trees, one live and two dead, occur on a north-facing slope of 30°, about 30 m N of summit "5696". The live tree measured 92.7 cm dbh and ca. 35 m height. Two adjacent standing dead trees have similar diameters, and bole char from a fire at least 100 years ago. A second live tree was located about 20 m upslope, measuring 28.9 cm dbh and ca. 15 m height. Field observations on 30 Mar 2003 confirmed that both live specimens survived the severest drought in more than a century. There was extensive mortality of *P. lambertiana* in other nearby ranges. The site is characterized by a mean annual precipitation of 80 cm (Minnich and Everett 2001, *loc. cit.*) and granite-derived soils. Associated species include *Quercus chrysolepis* Liebm, *Pseudotsuga macrocarpa* (Vasey) Mayr, *Pinus coulteri* D. Don, and *Abies concolor* (Gorden & Glend.) Lindley with no understory vegetation and abundant oak litter.

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WYOMING

TRIPLEUROSPERMUM MARITIMUM subsp. *INODORUM* (L.) Appleq. (ASTERACEAE).—Teton Co., south shore of Jackson Lake, east side of the Teton Mountains, T45N R115W sect. 24, weedy in cobble of lake shore, alt. 6800 ft., 20 July 1986. *L. M. Schultz & J. S. Schultz 10101* (UTC, NY, MO), det. W. L. Applequist (MO).

Previous knowledge. Usually recognized as a separate species, *T. inodorum* (L.) Sch. Bip. or *Matricaria inodora* L., incorrectly termed *M. perforata* Mérat in many floras, but probably better treated as a subspecies of *T. maritimum* (L.) W.D.J. Koch, aka *M. maritima* L. (see Applequist *in* Taxon 51:757–761. 2002). Native of Europe, naturalized as a weed of roadsides and waste places, said to be found primarily in the northeastern United States and Canada and sparsely in the Pacific states. Present distribution includes Idaho, Colorado, Nevada, South Dakota,

and North Dakota, as well as Utah and Montana. Plants of *T. maritimum* from the latter two states are described by Welsh et al. (Utah flora, 1993) and Lackschewitz (Vascular plants of west-central Montana, 1991) as weedy or robust plants up to 60 cm high. Those descriptions surely refer to subsp. *inodorum,* as *T. maritimum sensu stricto* is a smaller, often prostrate plant that favors saline environments; specimens identifiable as subsp. *inodorum* have been seen from both states (*Harvey 6943* [MO] from Missoula, Montana; *N. H. & P. K. Holgren 11266* [UTC] from Sevier Co., Utah; *B. Neely 676* [UTC] from Cache Co., Utah).

Significance. First unambiguous record for Wyoming, although *T. maritimum* is noted by Dorn (Vascular plants of Wyoming, 2nd ed., 1992); subsp. *maritimum* is specified by Nelson and Hartman (Checklist of the vascular plants of Wyoming, 1994). The fact that earlier references rarely mention subsp. *inodorum* under any name in the western United States suggests that its range has expanded rapidly in recent decades; for example, Harrington in 1964 (Manual of the plants of Colorado) says that only a single record from Colorado is known, whereas Weber in 2001 describes it as "abundant" (under the name of *M. perforata*; Colorado flora: western slope, 3rd ed.).

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MEXICO

CEANOTHUS PAPILLOSUS Torr. var. *ROWEANUS* McMinn (RHAMNACEAE).—Baja California, Valle Las Palmas region, Cerro Bola: just southwest of summit with communications towers along dirt road leading to the southwest at the head of Cañon La Piedra, near 32°18′49.7″N, 116°40′10.7″W, elev. 1158 m, 9 Apr 2001, *Steve Boyd, LeRoy Gross, Bart O'Brien, & Clem Hamilton 10349* (RSA); Valle Las Palmas region, Cerro Bola: ridgeline just southwest of summit with communications towers along dirt road leading to the southwest, near the head of Cañon La Piedra, near 32°18′52.5″N, 116°40′26.4″W, elev. 1176 m, 9 Apr 2001, *Steve Boyd, LeRoy Gross, Bart O'Brien, & Clem Hamilton 10350* (RSA).

Previous knowledge. Ceanothus papillosus var. *roweanus* is known from a disjunct population on ultramafic substrates in the vicinity of Pleasants Peak in the Santa Ana Mountains, Orange and Riverside counties, California (P. A. Munz 1974, A flora of southern California, University of California Press, Berkeley). Its core range is further to the north, in the coast ranges from northwestern Ventura County to San Benito and Monterey counties (M. Van Renssalaer and H. E. McMinn. 1942. *Ceanothus.* Santa Barbara Botanic Garden, Santa Barbara, CA; C. F. Smith 1998, A flora of the Santa Barbara region, California, Capra Press, Santa Barbara; P. A. Munz 1974, *loc. cit.*; C. Schmidt, pp. 932–938 in J. C. Hickman [ed.] 1993, The Jepson manual: higher plants of California, University of California Press, Berkeley).

Significance. The collections from Cerro Bola represent the first record of the taxon from Mexico, and a disjunction of ca. 186 km from the nearest known population in the Santa Ana Mountains.

—STEVE BOYD, LEROY GROSS, BART O'BRIEN, and CLEMENT W. HAMILTON, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

REVIEW

Cacti: biology and uses. Edited by Park S. Nobel. 2002. University of California Press, Berkeley, CA. 280 pp. Hardcover $65.00. ISBN 0-520-23157-0.

Cactus biology is a field that is experiencing a rush of recent interest in spite of a broad and deep canon of literature that has been accumulating for over a century. It is no small accomplishment, then, that Nobel has assembled a work that will stand as a primary utility for cactus biologists for some time. A diverse and international group of expert authors contribute here to a produce a more-or-less complete representation of the state of cactology at the turn of the millennium. Contributed chapters include up-to-date information on cactus systematics and evolution, anatomy and physiology, and diverse aspects of ecology and economic botany.

An understanding of the relationships among the cacti must underlie a synthesis of such diverse and specialized fields; this point is made in the preface (p. ix), and the first chapter (contributed by R. S. Wallace and A. C. Gibson) addresses the evolution and systematics of the Cactaceae. For the diverse audience (ecologists, environmentalists, agriculturalists, consumers, hobbyists, and enthusiasts; p. ix) addressed by this book, a clear and accurate synopsis of current cactus systematics is essential; chapter one succeeds in clarity for the most part, but has a few unfortunate misprintings and inaccuracies that may misrepresent cactus evolution to the broader audience. Contradictory inferences about the evolution of the subfamily Opuntioideae based on morphological and molecular evidence are not satisfactorily reconciled: The persistent leafiness of the genera *Austrocylindropuntia, Pereskiopsis,* and *Quiabentia* is cited as evidence of their obvious primitive status within the subfamily (p. 7), while later molecular analyses are presented as providing evidence of "a basal lineage for the subfamily (p. 14)" that includes leafy *Austrocylindropuntia* possibly nested within leafless *Cumulopuntia* (although *Pereskiopsis* and *Quiabentia* are represented as basal lineages within another (presumably derived) terete-stemmed clade of opuntioid cacti); This statement may be an over-interpretation of the data presented in fig. 1.5 (p. 15), in which the *Austrocylindropuntia-Cumulopuntia* lineage is one of five clades (including the two referred to above) that form an unresolved polytomy for the subfamily. The source of this molecular analysis is very difficult to pin down: in the text it is cited as "Dickie 1998," and "Dickie and Wallace 2001." Dickie 1998 is an unpublished master's thesis; Dickie and Wallace 2001 does not appear where it is cited (Systematic Botany), although in the references it is listed as "in review." In the figure caption for

fig. 1.5, the citation is given as "Dickey [sic] and Wallace 2000," which does not appear in the references ending the chapter. The actual source of the data discussed here is Wallace and Dickie (2002), which contains an identical cladogram to fig. 1.5. The caption for fig. 1.5 also presents the cladogram as a "strict consensus" tree, whereas the figure is labeled as a majority rule tree. As the topology is identical to that of Wallace and Dickie (2002), it is likely that the figure actually represents a majority rule tree, as it is cited there. One further series of minor misprints occurs in the citation of "Applequist [sic] and Wallace 2001" (p. 3, in the caption on p. 4, and in the lit. cited on p. 18; correctly cited as Applequist and Wallace, 2001), and in two of the cladograms printed (figs. 1.2 and 1.5), where some branches are missing. These errors and misprintings may not be the fault of the editor, but the responsibility of the publisher (P. M. Drennan personal communication).

In spite of the confusion caused by the above, chapter one does contain a great deal of useful and accurate information on cactus evolution and systematics. The authors discuss the dilemma of a monophyletic Cactaceae within a paraphyletic Portulacaceae, the subfamilial classification of cacti, and the recent decision to recognize subfamily Maihuenioideae. The discussion on the classification of subfamily Cactoideae is well written and well documented, and includes thoughtful discussion on the parallel evolution of epiphytic and columnar growth forms in the northern and southern hemispheres. The problem of choosing a morphologically primitive taxon among the Cactoideae for phylogenetic analyses is also well presented. If a second edition is issued, this chapter will remain a valuable reference with minimal revision.

Two excellent chapters provide contemporary summaries of above- (ch. 2) and below-ground (ch. 3) anatomy of cacti. A discussion of environmental biology (ch. 4) places this field in its historical context, highlighting the numerous contributions of the Carnegie Institution's Desert Botanical Laboratory, near Tucson, in the first half of the 20th century. A seemingly exhaustive list of abiotic factors affecting cactus growth and survival is thoroughly discussed. A summary of what is known about cactus reproductive biology (ch. 5) surveys the various procreative functions of the cacti, sexual and asexual.

A pair of chapters deals with the biotic ecology of the cacti, beginning with a survey of population and community ecology (ch. 6), and completed with an excellent chapter reviewing the documentation of vertebrate forage of *Opuntia* (ch. 7). This chapter is an extremely well presented, exhaustive

review of this phenomenon, which does much to challenge the popular dogma that cacti are well defended against herbivory.

A chapter (8) on the conservation issues related to cacti will likely reach its intended audience with this book. I applaud two positions taken by authors T. H. Boyle and E. F. Anderson here: that seed-grown cacti are better for the greenhouse hobbyist; and that the professional researcher should not be lumped with the profiteering wholesale collector.

The next five chapters deal with mankind's use of the cacti in agriculture and ranching. An excellent discussion (ch. 9) of the early domestication and diffusion of both opuntioid and columnar cacti throughout Mesoamerica and beyond stands as a wonderful synthesis of botanical, historical and archeological work. Here, authors A. Casas and G. Barbera present the most complete treatment of this subject to date. Following this is a summary on modern tuna (*Opuntia ficus-indica* fruit) production (ch. 10) that covers all aspects of this important crop, from site selection to storage physiology. A subsequent discussion (ch. 11) surveys other domesticated and semi-domesticated cactus fruit crops in the subfamily Cactoideae. A chapter (12) is devoted to the use of cacti as livestock forage in arid and semiarid regions, particularly in western Asia and North Africa. Finally (in ch. 13), a summary of nopalitos, mucilage, fiber, and cochineal (all

products derived from opuntioid crops) is presented.

Two final chapters finish the book: one on insect pests and diseases of cacti (ch. 14), which surveys all non-vertebrate predators of cacti, and their distributions, both natural and human-mediated; and a chapter (15) on breeding and biotechnology, which emphasizes the germplasm resources available as they relate to the fruit crops of the genus *Opuntia,* and the use of modern molecular and biochemical techniques to study these plants.

Although there are a few minor errors (detailed above), the group of authors brought together here has produced a reference that is certain to see a lot of use over the next decades. This book is an excellent resource for any botanist, and is invaluable to the student of cacti; my copy has already sprouted a dense interdigitation of yellow post-it notes.

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REVIEW

Geology and plant life: the effects of land forms and rock types on plants. By Arthur R. Kruckeberg. 2002. University of Washington Press, Seattle, WA. 362 pp. $35.00 ISBN 0-295-98203-9.

Art Kruckeberg's scientific life has revolved around the effects of lithology on plant evolution and distribution. Kruckeberg has authored dozens of papers on the subject, with a distinct focus on ultramafic ("serpentine") rock types and the Pacific Northwest. Beginning with his earliest published work, over fifty years ago, Kruckeberg has been in the forefront of the integration of geology and plant ecology. *Geology and plant life* is partly a summary of Kruckeberg's life work and partly a paean to his life-long fascination with rocks and plants.

In the mid-1980's, Kruckeberg developed the term "geoedaphics", which—in *Geology and plant life*—he suggests is a synonym of "geoecology", a well-developed field of study outside of the United States, but largely ignored here. "Geoedaphics" represent the field of study investigating the "reciprocal interactions of topography, lithology, and soils with flora and vegetation." Kruckeberg's new book is well-aimed and well-timed. Many of the most fundamental questions now facing humans and their present and future interactions with planet earth and its other denizens (e.g., global warming, air and water pollution, habitat alteration, mass extinction) will require answers that integrate across biological and physical sciences. The final chapter of *Geology and plant life* deals directly with some of these issues. Although the term "geoedaphics" may not ultimately make it into the dictionary (the term really only concerns a part of the larger and better developed field of geoecology, and the word unfortunately includes no etymological root referring to the biotic side of the discipline it represents), the message of this book will endure.

Geology and plant life is replete with photos; indeed there are nearly 100 of them, which is an extraordinary number for a book with 318 pages of text. A great number of the photos are excellent, but sadly they are all in black-and-white, and printed on the same paper as the text. One also can't help but wonder if a little money might have been saved (and used to fund a section of color plates?) by more thoughtful graphics editing. For example, there are fully nine photos of serpentine barrens, and some of the landscape photos are vague and not especially representative of the point Kruckeberg would like them to make. A number of photos are also nearly identical repeats of others, sometimes in the same photo suite. The number of Tables in *Geology and plant life* is impressive (nearly 50!), and with them, Kruckeberg does a nice job of summarizing large amounts of information in an easily digestible format. For instance, Chapter 5 ("The influences of lithology on plant life") provides a set of tables that cover everything from rock classification and molecular composition, to typical landforms, weatherability, and suitability for plant growth.

In Chapter 1 ("The geology–plant interface") Kruckeberg sets the stage and tone for the remainder of the book. This chapter is devoted largely to a laundry list of the ways in which geology *sensu lato* affects plant physiology, morphology, evolution, ecology, biogeography, etc. This is a nice summary of the myriad connections between geology and botany, but the format (and the fact that some of the major points are repeated multiple times) makes this section a somewhat difficult read. Kruckeberg's main point in this chapter—indeed, in the book—is that ecologists have historically focused their interests and research efforts on biotic interactions, and have largely ignored the abiotic side of their supposedly holistic discipline. In this assertion—in which he is entirely correct—he makes the same argument made by the European geoecologists. Kruckeberg pushes this point forcefully throughout the book.

Chapters 2 and 3 provide the "geoedaphic" background. Chapter 2 is a nicely written, concise account of the historical roots of geobotany, stretching from von Humboldt to Clements, Braun-Blanquet and Jenny. Chapter 3 ("Geoedaphics and other environmental influences") is only seven pages in length, and serves simply to set out the working hypotheses of "geoedaphics", namely: (1) geologic control of the biosphere is primary; (2) control by regional climate is primary only when geology does not influence regional climate; (3) edaphic controls are secondary for a given regional climate, but primary within that region. Kruckeberg argues at great length that Cain's dictum that "climate is primary" in determining plant distributions (a point made by just about every other phytogeographer as well) is not true, and that plant biogeography and just about everything else connected with plant life is in fact driven primarily by geology instead. When forced by his own reasoning to accede that global climates are palettes painted on regionally by topography and lithology, Kruckeberg plays trump by stating that the very existence of planet earth is a geophysical phenomenon. So there!

Chapter 4, entitled "Landforms and plant life", deals primarily with the influences of mountainous landforms on vegetation. Although it provides a decent overview of the subject, from my point of view this is the most unsatisfying of the book's

chapters. It is disappointing that Kruckeberg makes almost no reference to the extensive body of literature stemming from the work of European physical geographers and biogeographers from Alexander von Humboldt, to Carl Troll and Heinrich Walter. Troll in particular, the father of the fields of landscape ecology and geoecology, is afforded nary a citation, even though Troll is probably the single most important figure in the field of science studying the interactions between mountainous landforms and vegetation. Perhaps Kruckeberg's snubbing of these important figures is due to their focus on the importance of climate in driving vegetation patterns on earth, which contradicts his "geophilic" viewpoint. Either way, it is unfortunate, and detracts from the usefulness and credibility of this chapter. Another shortcoming of this chapter is Kruckeberg's almost complete reliance on material published before the 1990's. For example, no mention is made of Christian Koerner's fundamental work on high altitude plant ecology and treeline.

Chapter 5, "The influences of lithology on plant life", is the meat of *Geology and plant life,* and comprises fully 40% (126 pages) of the book's 318 pages of text. This is where Kruckeberg is most at home, and this is where he has the most to offer the reader. To a certain extent, I found myself wondering why Art didn't simply write a book called *Lithology and plant life,* as he does such a fine and thorough job of treating this subtheme. The chapter presents a detailed consideration of the effects of different substrates (granite, limestone, sandstone, shale, serpentine, gypsum—you name it) on worldwide vegetation. The section on serpentine is 42 pages in length and is especially complete (for obvious reasons!). There is also a section on rock weathering and soil formation, and a treatment of wetland vegetation as well. One of the most valuable features of this chapter is its worldwide scope. For example, informative summaries are provided of serpentine habitats in Cuba and New Caledonia, limestone floras in the European Alps, and karst vegetation on the Balkan Peninsula and in the Antilles. The citation list alone is worth the price of the book!

Chapters 6 and 7 deal with the effects of "geoedaphics" on plant evolution and distribution. "Implications of geoedaphics for systematics and evolution" (Chapter 6) is nicely organized, and written

for the layman. Kruckeberg's explanation of preadaptation and the acquisition of edaphic tolerance is especially well-presented, and appropriately simplistic. Chapter 7 ("Geoedaphics and biogeography") begins with a reprise of Kruckeberg's quixotic joust with the "climate is primary" folks, but soon drifts into more interesting realms. Separate sections treat the relationships between "geoedaphics" and plate movements, the vicariance-long distance dispersal debate, climatically-created landforms, biogeomorphology, island biogeography, and historical biogeography. The chapter ends with a brief consideration of the importance of discontinuous habitats for the distribution of edaphic endemics and patterns of species diversity.

The final chapter is a summary of some of the influences of man on the geology-plant interface. It is always difficult to write about man's impact on the planet without getting a little angry, but Kruckeberg does a good job of searching for positive things to highlight, such as The Nature Conservancy efforts in northern California, and the preservation of Dun and Red Mountains in New Zealand. On the other hand, it should also be noted that some of Kruckeberg's worries may be slightly overstated. For example, his concern that "preservation of serpentine habitats in California is spotty, inadequate, and largely coincidental" seems to be based on an incomplete knowledge of California conservation units. Kruckeberg states that only one preserve in the state has been established specifically for "the full display of the serpentine syndrome", but in reality there are quite a number of serpentine reserves in California, regardless of why they were established. In the Forest Service alone we manage at least a half-dozen Research Natural Areas on serpentine, and about a dozen Botanical Special Interest Areas as well. This is not to say that coverage is completely "adequate" (nor protection complete), but—at least in parts of California—the situation may not be quite so dire as Art portrays.

Overall, *Geology and plant life* is a fine book, and a very approachable overview of the intersections between geology and the plant sciences. It is very affordable for a hard cover text of this size (only $35.00 last I checked!), and a great purchase for anyone interested in any aspect of plant ecology.

—HUGH D. SAFFORD, USDA-Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592.

RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Jason Alexander, currently a graduate student in the Department of Botany & Plant Pathology, Oregon State University, is the recipient of the Rupert Barneby Award for the year 2003. Mr. Alexander will be studying the systematics of various species of *Astragalus* in the western United States.

The New York Botanical Garden now invites applications for the Rupert Barneby Award for the year 2004. The award of US$ 1000.00 is to assist researchers to visit The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a detailed letter describing the project for which the award is sought, and the names of 2–3 referees. Travel to the NYBG should be planned for some time in the year 2004. The application should be addressed to Dr. James L. Luteyn, Institute of Systematic Botany, The New York Botanical Garden, 200th Street and Kazimiroff Blvd., Bronx, NY 10458-5126 USA, and received no later than December 1, 2003. Announcement of the recipient will be made by December 15th.

Anyone interested in making a contribution to THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Luteyn.

INFORMATION FOR CONTRIBUTORS

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Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE-SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, five key words or phrases, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or 'erasable' paper. Avoid footnotes except to indicate address changes. Abbreviations should be used sparingly and only standard abbreviations will be accepted. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units, except specimen citations, which may include English or metric measurements. Authors are encouraged to include the names, addresses, and e-mail addresses of two to four potential reviewers with their submitted manuscript.

Authors of accepted papers will be asked to submit an electronic version of the manuscript. Microsoft Word 6.0 or WordPerfect 6.0 for Windows is the preferred software.

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Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used by Sivinski, Robert C., in MADROÑO 41(4), 1994. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 8th ed. Names of authors of scientific names should be abbreviated according to Brummitt and Powell, Authors of Plant Names (1992) and, if not included in this index, spelled out in full. Titles of all periodicals, serials, and books should be given in full. Books should include the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted 5 free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $40 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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NOTES

BOOK REVIEWS

A CATALOG OF THE MOSSES OF SANTA CRUZ COUNTY, CALIFORNIA

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Abstract

One hundred ninety species and one variety of moss are documented in Santa Cruz County, California representing 32% of the California moss flora. Several aquatic species expected to be found are absent. Fourteen species are new records for the central coast of California. One hundred five species are reported in Santa Cruz County for the first time. Two species, *Fissidens taylorii* C. Müll. and *Archidium alternifolium* (Hedw.) Schimp. are reported new for California.

Key Words: Bryophytes, Moss, Santa Cruz, California.

As part of a larger effort to more fully understand distribution patterns of bryophytes in California, it has become necessary to systematically and carefully catalog smaller geographical regions and political entities. Several collectors are contributing in this regard: David Toren in Lake and San Francisco Counties, James Shevock in the Sierra Nevada and San Francisco County, Paul Yurky in Marin County, and Alan Whittemore in San Mateo County. This study is an effort to fill in the void for Santa Cruz County, and by extension, the central coast of California.

Santa Cruz County is located approximately 125 kilometers south of San Francisco on the California coast. (See statewide map, inset, Fig. 1.) The land rises from the Pacific Ocean and Monterey Bay through coastal escarpments to rather steep-sided mountains forming the inland boundary with neighboring counties. The county covers approximately 1142 square kilometers. According to the 2000 U.S. census, the population is 225,640. Elevation ranges from sea level to 978 m.

Climate

The climate of Santa Cruz County is essentially Mediterranean, with mild, but wet winters, and moderate summer temperatures. Marine fog is common in immediate coastal areas in the summer, further moderating temperatures. Average rainfall varies greatly throughout the county. According to Thomas (1961), the City of Santa Cruz receives an average 71 cm. The California Department of Forestry reports a 15 year average of 115 cm, with a maximum of 228 cm, in Felton, a town in the San Lorenzo River Valley (unpublished data). Virtually all precipitation falls in the form of rain between late October and early May. Snow is uncommon, usually only on the highest ridges, and melts within days. In spite of the annual summer drought, there are several year round waterways draining the mountain areas. Although small panels of ice may temporarily form along the edges of slow moving creeks, no waterway in Santa Cruz county freezes

over for the winter. It is also important to note that the vast majority of the moss substrate stays dry throughout the summer.

The amount of rainfall and the length of the rainy season decrease steadily from the temperate rainforests of southern coastal Alaska, British Columbia and Washington State, south to the fog deserts of Baja California. The coastal counties of San Francisco, San Mateo, and Santa Cruz mark the approximate midpoint to this gradient. Smaller scale variations within the county are also important to note. As elevation increases, the frequency of marine fog decreases, but the amount of rainfall increases. The uninterrupted ridge of Ben Lomond Mountain creates a fog shadow in the San Lorenzo River Valley. Shade created by tall redwood trees moderates hot summer temperatures. Cold air sinks into steep river canyons. Combinations of these geographical and meteorological factors create microclimates of all descriptions.

The effect of marine fog on temperature has already been mentioned, but it also has an important effect on water distribution. As the fog blows inland off the ocean, it condenses on the leaves of trees and falls to the forest floor. Fog drip has been measured by Oberlander (1953) for a five week period from July 20 to August 28, 1951 in nearby San Mateo County. It ranged from 4.5 cm under a *Sequoia sempervirens* (D. Don.) Endl. (coast redwood) to 149 cm under a *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. (tanbark oak). The large difference was explained by the degree of protection from the prevailing winds. Nevertheless, it is clear that fog can be a significant source of moisture during the summer months.

Major Plant Communities

Second growth redwood forests are the signature plant community of the county. A typical coast redwood forest includes *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. (tanbark oak), *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir), *Umbellularia californica* (Hook. & Arn.) Nutt. (California
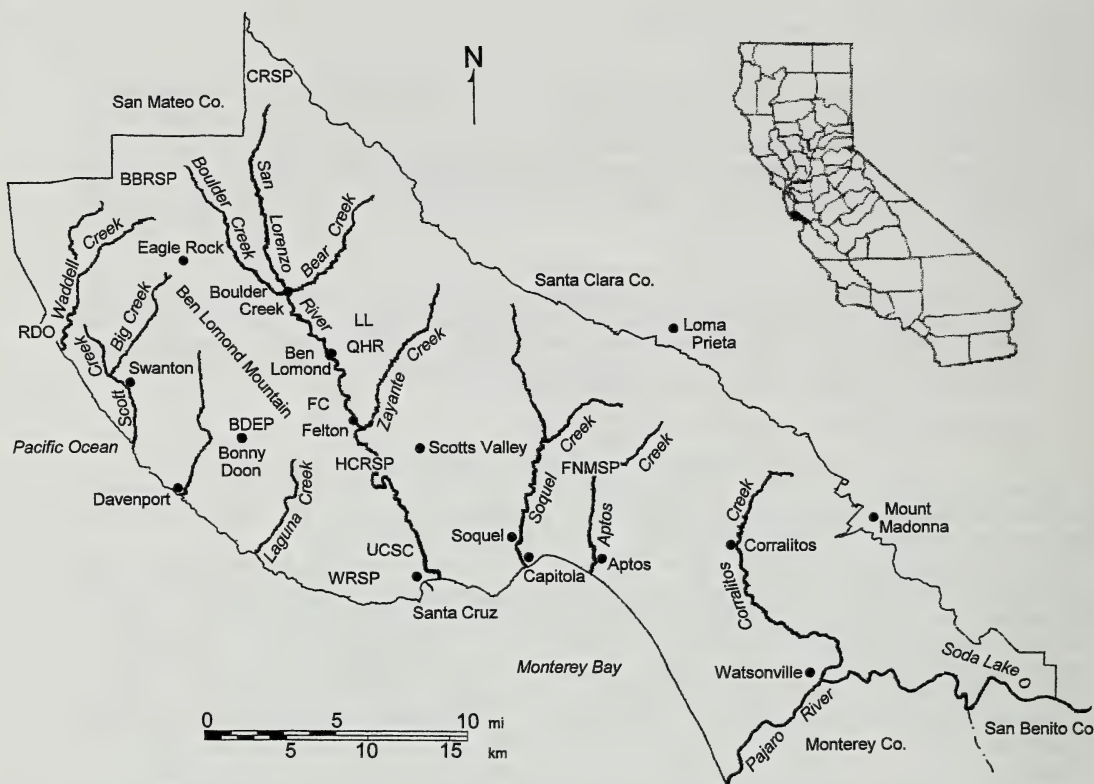
FIG. 1.   Place name map of Santa Cruz County. Inset: County map of California showing Santa Cruz Co. darkened.

bay), and often *Acer macrophyllum* Pursh (big-leaf maple), as well as the coast redwood. Redwood forests are generally limited to areas away from the immediate coast where summer fog is frequent. Only two patches of old growth redwood forest survived the 19th century logging in the county: one in Henry Cowell Redwoods State Park, and the other in Big Basin Redwoods State Park.

Equally important plant communities are mixed evergreen forests, and chaparral. Mixed evergreen forests are dominated by either *Quercus agrifolia* Nee (coast live oak) or *Quercus wislizenii* A.DC. (interior live oak), *Arbutus menziesii* Pursh. (madrone) and Douglas fir. The under story often includes *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene (poison oak), and *Rubus ursinus* Cham. & Schldl. (California blackberry). Mosses in the mixed evergreen forests are mostly epiphytic or along the soil banks of trails and roads. Chaparral is a scrub community often centered around various species of *Arctostaphylos* spp. (manzanita), *Ceanothus* spp., *Adenostoma fasciculatum* Hook. & Arn. (chamise), *Artemisia californica* Less. (California sage) and *Pickeringia montana* Nutt. (chaparral pea). Occasionally, stands of the fire dependant *Pinus attenuata* Lemmon (knobcone pine) are interlaced with the chaparral. Mosses in the chaparral tend to be found on the poor soils and rock

outcrops that are common in this habitat, or on the trunks and branches of the shrubs themselves. Both of these communities are dryer than the redwood forest.

Grasslands are prominent along the hillsides of the north coast, dominated by non-native species. Coastal California grasses generally die back in the summer due to lack of rain. This mostly limits the mosses in this community to the winter ephemerals, which complete their life cycle while the soil is still moist and before the new year's growth cuts off the sunlight.

One other small plant community deserves mention here. The ponderosa pine parklands of the inland marine sand deposits of Ben Lomond and Bonny Doon support a well- documented vascular endemic community (Marangio 1985). The sandstone rocks that punctuate the sandy soil here are the only known sites for *Grimmia ungeri* and *G. montana* in the county.

Agriculture dominates the immediate coastal areas outside the greater Santa Cruz City area, as well as the majority of the Pajaro River Valley near Watsonville. Unfortunately, freshwater sloughs around Watsonville are almost devoid of bryophytes. It seems probable that agricultural runoff is limiting bryophyte growth in this area.

Geology

The geology of the Santa Cruz Mountains is quite complex. The county is crisscrossed with faults that have exposed various rock formations. However, for the purposes of this study, surface conditions are paramount and it can be simply said that the vast majority of exposed rock surfaces in Santa Cruz County are sedimentary rocks deposited in the Tertiary period (Brabb 1989). These are primarily sandstone and mudstone. The only exposed granitic rock is found on Ben Lomond Mountain, with the majority of that being found in creek beds and canyons. The Watsonville area is dominated by various alluvial, colluvial and eolian deposits from the pleistocene epoch (Brabb 1989).

Along the southern flank of Ben Lomond Mountain, there are pockets of exposed mesozoic or paleozoic marble. Between 1870 and 1919, these were exploited in the production of lime for the cement industry. This provides calcareous habitats for various mosses, both terrestrial and aquatic. The largest of these, in the Fall Creek division of Henry Cowell Redwoods State Park, and on the campus of the University of California at Santa Cruz, are actually abandoned quarries. Calcareous rock is also exposed along Eureka Canyon Road, and near the mouth of Yellow Bank Creek.

Collection History

There is a rich history of bryophyte collection along the central coast of California (Thiers and Emory 1992). During the winter of 1792 to 1793 Menzies' ship, H.M.S. Discovery, was stationed in Monterey, a port on the southern tip of Monterey Bay approximately 45 km south of Santa Cruz County. During that stay, he explored the central coast, and even made an overland trip to San Francisco. This would very likely have taken him through present day Santa Cruz County. Unfortunately, label information is insufficient to prove any of his collections were obtained within Santa Cruz County. Other botanical collectors centered their work around either Monterey or San Francisco, but again no collections from this early period can be definitely attributed to the county. The oldest collection definitely traceable to Santa Cruz County is a sample of *Epipterygium tozeri* made in 1893 by Michener & Bioletti, although some argument could be made to include a collection of *Orthotrichum papillosum* (as *O. lyellii*) made in 1888 by L. M. Underwood. The location on the latter collection is given as "Santa Cruz Mountains" which run from San Francisco County south to northern Monterey County.

In more recent times, only sporadic and short-term visits have been made to the county by a variety of collectors. The most notable among these are W. B. Schofield (31 collections on 10 dates between 1956 and 1966), D. H. Norris (75 collections on 5 dates between 1980 and 1995), A. Whittemore (38 collections on 13 dates between 1989 and 1999), S. Flowers (16 collections on 2 dates in 1957), J. H. Thomas (39 collections on 16 dates between 1950 and 1965), J. T. Howell (22 collections on 2 dates in 1949 and 1950), and L. Koch (6 collections on 3 dates between 1947 and 1950). Most of these efforts have been centered in the county's state parks. Until this study, there has never been a concentrated effort to inventory the bryophytes of Santa Cruz County.

METHODS

Moss collections were gathered by the author from 1996 to 2003, from all sections and elevations throughout the county. Many locations were visited more than once, at different times of the year. Collection data includes latitude and longitude, elevation, substrate and habitat. Since 1999, latitude and longitude were determined with a handheld global positioning system (GPS) receiver. Prior to 1999, latitude and longitude were estimated with the use of US Geological Survey topographic maps. Elevations have been determined from the same topographic maps on CD ROM produced by TOPO (1999). These collections are mostly housed in the California Academy of Sciences (CAS).

I have cataloged and examined all specimens in Bay Area herbaria (CAS, UC, SFSU). Other herbaria housing Santa Cruz mosses include ALTA, BUF, CAN, MICH, MO, NY, and UBC. The collections of Leo Koch reside in ILL. Although many of his collections are duplicated in CAS and UC, I expect a certain number of collections from Santa Cruz might be found there. Unfortunately, I have been unable to confirm this. The same must be said of Whittemore's collections in MO. Collections cited from UBC and NY have been downloaded from an on-line database, and have consequently not been examined. All collections and their label data were entered in a computer database.

With only one exception, no unexamined specimen has been cited in this paper as evidence of a taxon's presence in the county unless it has been corroborated by another collection that I have examined. The only exception is Koch's collection of *Fontinalis neomexicana*. This specimen was cited as a "specimen examined" in Welch's monograph on the genus (Welch 1960). The generally accepted concept of this species has not changed since 1960 so Welch's citation makes the determination certain.

Identification of specimens has been accomplished using various moss floras from North America and beyond (Lawton 1971; Flowers 1973; Smith 1978; Crum and Anderson 1981; Ireland 1982; Sharp et al. 1994). Dan Norris and Jim Shevock helped to sort out unfamiliar taxa. Difficult collections were sent to appropriate authorities for confirmation or determination.

TABLE 1. PRIOR STATUS OF THE UNDESCRIBED MOSS TAXA FOUND IN SANTA CRUZ COUNTY. See Appendix II for more information on these taxa.

Taxon	Prior status
Bryum sp. A	Apparently new to science.
Bryum sp. B	Previously collected but unrecognized.
Orthotrichum sp. A	New to science.
Schistidium sp. A	Widely collected in California and beyond.
Schistidium sp. B	Widely collected in California and beyond.
Tortula sp. A	Known from 1986 in Tehama Co. and from San Luis Obispo Co.
Taxiphyllum sp. A	Apparently new to science. No *Taxiphyllum* is known from CA.

RESULTS

One thousand, seven hundred and twenty-six (1,726) collections were cataloged in the database of which 1,385 were made by the author. One hundred ninety (190) species, and one variety, in 87 genera were documented in Santa Cruz County, (see Appendix 1) representing 32% of the California moss flora. Of the 191 taxa, 86 were collected prior to this study, thus 105 taxa are reported new to Santa Cruz County. Of those 105, 14 are reported new to the central coast of California. (see Appendix I) Two of these 14, *Fissidens taylorii* C. Müll. and *Archidium alternifolium* (Hedw.) Schimp., are reported from California for the first time.

Seven taxa, one of which was collected in Santa Cruz County prior to this study, are presently undescribed. These will be described by various authors in other publications.

The catalog is divided into four sections. All are sorted alphabetically by genus and then species. Appendix I lists all described species and varieties that have been inventoried for Santa Cruz County. It includes a subjective assessment of the abundance of the species, a short description of the habitats of the moss, regularity of sporophyte occurrence, and a few representative collections illustrating the range of the species. Emphasis for the selection of cited collections is given to those locations that are politically protected and likely to remain ecologically intact for the foreseeable future. Collections have also been chosen to highlight earlier records, elevational extremes, variation in habitat, and those by a variety of collectors.

Subjective abundance is identified as follows: **Rare,** found only once or twice in the county and not known in large quantities from neighboring counties; **Occasional,** found occasionally within appropriate habitat; **Common,** often found within appropriate habitat; **Very common,** almost always found within appropriate habitat; **Abundant,** always found in large quantities within appropriate habitats. This information comes from the author's experience in the county and from discussions with local bryologists collecting outside Santa Cruz County. Whereas the number of collections examined is commonly used as an indication of abundance, that number can be misleading. Often collections are made in the field because two species

are macroscopically similar, thus overemphasizing the relative abundance of one or the other. Similarly, certain occasional and distinctive species (*Hedwigia* for example) are generally collected every time they are encountered, while easily recognized abundant species are often under collected. Ephemeral mosses are especially difficult to place in categories of abundance, because they can only be found during a certain time of year. Adding to the difficulty, certain ephemeral species may be common in one year and rare in the next.

Collection data are listed as follows: political name of site where applicable (i.e., state park name), short site description, year, elevation when available, collector, collection number, and herbarium. Collections by the author are designated by the initials *KMK*. For the most part, nomenclature follows Crosby et al. (2001). Where I have deviated from that work, I have added a note to explain my reasoning. Abbreviations for collection sites are as follows: Big Basin Redwoods State Park (BBRSP), Bonny Doon Ecological Preserve (BDEP), Castle Rock State Park (CRSP), Fall Creek Division of Henry Cowell Redwoods State Park (FC), Forest of Nisene Marks State Park (FNMSP), Henry Cowell Redwoods State Park (HCRSP), Loch Lomond Reservoir (LL), New Brighton State Beach (NBSB), Quail Hollow Ranch County Park (QHR), Rancho del Oso division of Big Basin Redwoods State Park (RDO), University of California at Santa Cruz (UCSC), Wilder Ranch State Park (WRSP). Locations for these sites can be seen in Fig. 1. For an interesting discussion of sites mentioned in the catalog, see Clark (1986).

Appendix II is an annotated list of the undescribed species found in the county. No attempt is made to describe these taxa, and their final status is subject to further investigation. Some of these mosses have been known to local collectors for years without being described; others are new to science. Table 1 lists the prior status of each of these taxa.

Appendix III is a short list of mosses that might reasonably be expected to be found in Santa Cruz County, but have yet to be collected. Plants are included in this section if they have been collected in nearby counties, and appropriate habitat exists in Santa Cruz County, or if a taxon is cited in a pub-

lication, and I have been unable to corroborate the record. Due to the general lack of knowledge of the distribution of California mosses, it would not be surprising to find these taxa in the county as well as others that are not on this list.

Appendix IV lists mosses by several habitat types. Some of the mosses reported from each habitat are not necessarily associated with that habitat but have been found in that habitat in Santa Cruz County.

DISCUSSION

It is evident that the limited collection history in Santa Cruz County has resulted in a limited knowledge of the moss flora. Seven species found in the county are as yet undescribed. Fifty-five percent of the mosses cataloged were not collected from Santa Cruz County prior to this study. The fourteen mosses that are new to the Central Coast represent major range extensions for their respective taxa. It remains to be seen if these collections represent continuous range extensions or disjunct populations.

The position of Santa Cruz County in the approximate center of the Pacific coast rainfall gradient has several implications. Dry land species, although present, are sporadic in distribution and only represented by a few collections from small populations. This is the case with such taxa as *Aloina rigida, Crossidium aberrans, C. squamiferum, Didymodon norrisii, Grimmia ovalis,* and *G. laevigata.* Conversely, species adapted to much higher humidity, which are common farther north, are absent. Santa Cruz County marks, to the best of my knowledge, the cismontane southern limits of *Hypnum circinale, Pseudotaxiphyllum elegans, Polytrichastrum alpinum,* and *Dicranum fuscescens.* Furthermore, the lack of summer rain and the steep terrain limits the occurrence of fresh water wetland. Thus habitat is limited for such species as *Aulacomnium palustre,* which is represented by only a single collection. There is no *Sphagnum* within Santa Cruz County at all.

The Mediterranean climate also allows for a rich suite of species that inhabit the trunks of trees. Many hardwood tree trunks, and even some Douglas firs are completely covered in mosses, and many of the epiphytic mosses (*Alsia californica, Dendroalsia abietina, Isothecium myosuroides* for example) are abundant. Temperatures are cool in the winter when the bark is wet, providing ideal conditions for bryophyte growth. Higher temperatures are present only in the summer when the mosses are protected by desiccation (Shaw and Goffinet 2000). This is not the case in the Sierra Nevada where epiphytic mosses are limited by a lack of available water in the winter, and in the summer, when occasional storms do bathe the trunks, temperatures are too high for optimal growth.

As mentioned above, there are many year-round creeks and two year-round rivers draining the Santa Cruz Mountains. It is interesting to note, however, that the aquatic bryoflora is rather limited in the county. Although *Platyhypnidium riparioides* and *Hygrohypnum bestii* have been collected, the former is rare and the latter is occasional. All but one collection of these two taxa are from creeks draining the southern and western flanks of Ben Lomond Mountain. *Fontinalis neomexicana* is only represented by one historical collection and was not relocated during this study. No other species of *Fontinalis* or *Hygrohypnum* have been collected nor has any species of *Scouleria* or aquatic *Schistidium* ever been documented in Santa Cruz County. Another interesting absence (in natural settings) is *Didymodon tophaceus,* a well-known calciphile, despite ample calcareous streams.

Two, as yet untested hypotheses, may explain the poor aquatic showing: the first deals with water temperature, and the second involves pollution and disturbance. It is possible that water temperatures are too warm for ideal growth since there is no significant snow melt to keep temperatures down throughout the year. It is also probable that water pollution is partially to blame. There has been a great deal of residential development and road building along many waterways, and it is likely that the cumulative effects of this construction has had significant impacts on the nearby streams. The fact that all of the creeks that do support aquatic mosses are fed from lightly populated areas supports this hypothesis.

Ephemeral mosses are well represented in Santa Cruz County. *Ephemerum serratum, Tortula acaulon,* and two species of *Pleuridium* were found consistently throughout the county over the entire span of this study. *Acaulon muticum,* however, was widespread over the county in 2002 (nine locations), but not found in any other year despite repeated attempts to relocate this moss in 2003. All of the *Microbryum* specimens were also collected in 2002. It is possible that these taxa just eluded me during the previous five years of collecting, but it seems more likely that 2002 was meteorologically perfect for their development. It is much more difficult to generate similar hypotheses for the ephemeral taxa that have only been collected from one or two locations. *Archidium alternifolium* and *Entosthodon attenuatus* fall into this latter category.

It is worth discussing the mosses that grow along the immediate shore, an area that I define as being on the beach or on the first coastal bluff overlooking the beach. On a large scale, this habitat is under the influence of air born salt, especially in the winter when storms lash the coast. My assumption was that this would limit the flora to a certain number of "tolerant species". The only moss that is consistently associated with the coast is *Mielichhoferia elongata.* That species is found inland, but is rare there and definitely increases in occurrence as one nears the ocean. Other species collected in this zone are specialists in disturbed areas (*Bryum barnesii,*

B. gemmilucens, Didymodon vinealis, Funaria hygrometrica) indicating a tolerance for a wide variety of microhabitats, and these species are widespread throughout the county. *Homalothecium arenarium* and *Scleropodium californicum* are associated with chaparral and other scrubby habitats, and they are found along the coast where coastal scrub is dominant. *Amblystegium juratzkanum, Eurhynchium praelongum,* and *Bryum gemmiparum* were found near fresh water in areas that might be inundated, but were more often only moist or wet, again reflecting their inland preferences. So it appears that if the appropriate microhabitat exists along the shore, then any given moss suited to that microhabitat might be found there, uninhibited by the salt air.

Most of the collections from Santa Cruz County prior to this study were from Big Basin Redwoods State Park. Including Eagle Rock, Big Basin is the center of moss diversity within the county. Of the 191 taxa listed for the county, 100 are known from Big Basin. The only historical record that was not relocated during this study, *Fontinalis neomexicana,* was collected in Big Basin. The West Waddell Creek watershed in Big Basin, is home to all four mosses whose southern distributional limits were discussed above. Eagle Rock is no less remarkable. Despite its proximity to the coast, its flora includes mosses like *Didymodon norrisii, Grimmia laevigata, G. ovalis, Crossidium squamiferum,* and *Schistidium sp. A,* all xerophytic mosses usually associated with more inland habitats.

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APPENDIX I

CATALOG

Taxa preceded by an asterisk (*) denote those not known to have been collected from Santa Cruz County prior to this study. Those marked with a double asterisk (**) denote taxa not previously collected from the central coast of California (Marin, San Francisco, San Mateo, Santa Cruz, Monterey, Napa, Sonoma, Alameda, Contra Costa, Santa Clara Counties). Those marked with a triple asterisk (***) denote taxa that are reported new to California. Controversial or recently changed names are listed below the name that has been accepted for the taxon.

* *Acaulon muticum* (Schreber ex Hedw.) C. Müll.

Common in December to February in 2002; on quick drying, fine-grained soil in grasslands. Sporophytes on all collections.

On thin soil over mudstone in coastal pasture north of Davenport, 2002, 55 m, *KMK 2098* (CAS); on mineral soil of dirt road through pasture in Felton, 2002, 100 m, *KMK 2110* (CAS); on mineral soil in grassland opening near pond in meadow north of Scotts Valley, 2002, 215 m, *KMK 2116* (CAS).

* *Aloina aloides* (J. Koch ex Schultz) Kindb.

Occasional; on disturbed soil. Sporophytes common.

On disturbed soil near Pajaro River south of Watsonville, 2001, 5 m, *KMK 2051* (CAS); on sandstone road bank along Rte 152 northeast of Watsonville, 2001, 260 m, *KMK 2078* (CAS); UCSC, on soil in grassland at top edge of marble outcrop, 2002, 100 m, *KMK 2124* (CAS).

Note: all specimens with mature capsules can be referred to var. *ambigua* (B.S.G.) Craig.

* *Aloina rigida* (Hedw.) Limpr.

Rare; on sandstone rock outcrop in chaparral. Sporophytes found on this one collection.

BBRSP, on sandstone rock in chaparral, 2001, 575 m, *KMK 1307* (CAS).

Alsia californica (Hook. & Arnott) Sull.

Abundant; on the bark of trees, occasionally on rock under trees. Sporophytes common.

On dry sandstone in shade, 1957, *Flowers 5048* (ALTA); FNMSP, on bark of *Lithocarpus* in redwood forest, 1992, 90 m, *Whittemore 4043* (CAS, UBC); QHR, on trunk of *Quercus agrifolia* in diffuse light, 1996, 230 m, *KMK 305* (CAS); HCRSP, on trunk of *Quercus agrifolia* in diffuse light near the campground, 200 m, 1999, *KMK 642* (CAS).

* *Amblystegium juratzkanum* Schimp.

Common; on soil, rocks, or wood where continuously wet. Sporophytes unknown from county.

QHR, on wet stick in swamp near parking lot, 1996, 150 m, *KMK 243* (CAS); FNMSP, on wet soil at redwood tree base in Whites Lagoon, 1999, 430 m, *KMK 777* (CAS); WRSP, on granite rocks in Wilder Creek, 1999, 45 m, *KMK 825* (CAS).

Note: Although this taxon is commonly synonymized with *A. serpens,* the plants in Santa Cruz County show a consistent differentiation. This genus is noted for its intergradations between species (Flowers 1973), and this couplet is no different.

* *Amblystegium serpens* (Hedw.) Schimp. in B.S.G.

Common; On moist soil or wood around water, but also found as a lawn weed. Sporophytes occasional. Pinto Lake County Park, a shaded lawn weed, 1999, 60 m, *KMK 716* (CAS); WRSP, on thin moist soil on creek bank, 1999, 30 m, *KMK 830* (CAS); on mossy bank planted with shrubs in Santa Cruz, 2001, 25 m, *KMK 1295* (CAS).

Amphidium californicum (Hampe ex C. Müll) Broth.

Occasional; on shaded rocks. Sporophytes unknown from county.

BBRSP, forming tufts on dry sandstone cliff face, 1959, *Schofield & Thomas 11198* (UBC); HCRSP, on dry rock cliff face above railroad tracks, 1999, 90 m, *KMK 647* (CAS); on soil of irrigated garden bed in shade, Scotts Valley, 2000, 210 m, *KMK 1193* (CAS).

Anacolia menziesii (Turn.) Par.

Common; on shaded rocks of road cuts or outcrops in forest. Sporophytes occasional.

On dry roadside rock in mixed forest on Summit Road west of Maymens Flat, 1999, 875 m, *KMK 744* (CAS); BBRSP, on soil over sandstone outcrop in Slippery Rock Meadow, 2000, 380 m, *KMK 1333* (CAS); CRSP, on shelf of outcrop in chaparral, 1986, *Schofield 87755* (UBC); FC, on walls of lime kilns near the south fork of Fall Creek, 1997, 240 m, *KMK 354* (CAS); BBRSP, on sandstone outcrop in chaparral, 2001, 685 m, *KMK 1465* (CAS).

All fertile material of *A. menziesii* collected in Santa Cruz County can be referred to var. *baueri* Hampe.

** *Anomobryum julaceum* (Schrad. ex Gärtn. et al.) Schimp

Occasional; on moist sandstone rock banks. Sporophytes unknown from county.

QHR, on sunny sandstone wall that is wet in winter and spring, 1996, 235 m, *KMK 193* (UC); BBRSP, on sheltered vertical sandstone outcrop in chaparral, 2001, 570 m, *KMK 1314* (CAS); on vertical, shaded, soil bank near Bonny Doon, 2001, 390 m, *KMK 1455* (CAS); on sandy soil in sloping grassland above Soquel-San Jose Road, 2003, 260 m, *KMK 2835* (CAS).

Note: *KMK 2835* has brood branchlets which are quite rare in the west.

Antitrichia californica Sull. in Lesq.

Common; on the bases of *Quercus,* or on rocks in diffuse or full sunlight. Sporophytes occasional.

CRSP, on rocks of road cut on Summit Rd, just east of park entrance, 1999, 915 m, *KMK 734* (CAS); QHR, on lower trunk of *Quercus agrifolia,* 1996, 215 m, *KMK 303* (CAS); FC, on rock near Blue Cliff in diffuse light, 1999, 245 m, *KMK 659* (CAS).

*** *Archidium alternifolium* (Dicks. ex Hedw.) Schimp.

Rare, on thin wet soil. Sporophytes present on this one collection.

WRSP, on thin wet soil over sandstone near a spring in grassland, 2002, (CAS). [Confirmed by J. Spence.]

Atrichum selwynii Aust.

Common on soil of roadside and trailside banks in the shade. Most often found in redwood forests. Sporophytes occasional.

QHR, vertical sandstone wall above creek in forest, 1996, 210 m, *KMK 149* (CAS); WRSP, on sandy bank at chaparral-redwood forest boundary, 2000, 200 m, *KMK 960* (CAS); FNMSP, soil bank near stream in redwood forest, 1996, 490 m, *Whittemore 4041* (CAS); moist soil bank in redwood forest, 1994, 200 m, *Norris 82264* (UC); FC, on soil along Fall Creek, 1961, 190 m, *Thomas 8967* (CAS).

Atrichum undulatum (Hedw.) P. Beauv.

[*A. oerstedianum* (C. Müll.) Mitt]

Easily confused with *A. selwynii.* Abundance is difficult to determine, but in the same habitat as that species. Sporophytes occasional.

FC, along Fall Creek, 1961, 190 m, *Thomas 8937* (CAS); QHR, sandstone bank in mixed evergreen forest, 1996, 200 m, *KMK 300* (CAS); roadside bank in redwood forest, 2000, 270 m, *KMK 896* (CAS); soil bank in redwood forest, 1995, 160 m, *Norris 86864* (UC); BBRSP, soil bank, 1970, *Franck s.n.* (UC).

Aulacomnium androgynum (Hedw.) Schwägr.

Common; on rotting wood in redwood forests, or on soil or rock in chaparral. Sporophytes common.

FNMSP, on redwood log near Aptos Creek at Loma Prieta Mill site, 1997, 40 m, *KMK 379* (CAS); HCRSP, common on soil in chaparral along Pine Trail, 1999, 195 m, *KMK 645* (CAS); BBRSP, on charred redwood stump near Blooms Creek, 2000, 305 m, *KMK 1148* (CAS).

Aulacomnium palustre (Hedw.) Schwägr.

Rare; on hummock in swamp. Sporophytes unknown in county.

FNMSP, on small grassy hummock at the west end of White's Lagoon, 1999, 435 m, *KMK 1812* (CAS).

Barbula convoluta Hedw.

Common; on soil in gardens and other disturbed places. Sporophytes rare.

On moist, bare soil near beach in Capitola, 2000, 15 m, *KMK 1198* (CAS); roadside of Highway 9 in redwood forest north of Boulder Creek, 1954, 550 m, *Thomas 3666* (CAS); on shaded brick chimney in redwood forest near Felton, 1949, *Howell 295* (CAS); On non-irrigated garden soil in Santa Cruz, 2001, 35 m, *KMK 1246* (CAS).

* *Barbula unguiculata* Hedw.

Common; in irrigated gardens at commercial buildings, calcareous soils, and disturbed places. Sporophytes rare.

On shaded bare soil in garden in Felton, 2000, 90 m,

KMK 1182 (CAS); on shaded moist soil at base of tree in planting area in Scotts Valley, 2000, 175 m, *KMK 1179* (CAS); UCSC, on disturbed soil near the Barn Theatre, 2002, 100 m, *KMK 2275* (CAS).

* *Bartramia stricta* Brid.

Occasional; found on sandstone outcrops in meadow or chaparral, or on soil in grassland, often in full sun. Sporophytes occasional.

BBRSP, on sandstone outcrops in Slippery Rock Meadow, 1999, 365 m, *KMK 697* (CAS); WRSP, on bare soil in the middle of a deer trail in a meadow near the northernmost reservoir, 1999, 65 m, *KMK 833* (CAS); on soil bank at meeting between grassland and chaparral near the top of the hill above Scotts Valley High School, 2001, 250 m, *KMK 1335* (CAS).

* *Bestia longipes* (Sull. & Lesq.) Broth.

Common; on rocks or tree bases, usually near streams. Sporophytes unknown from county.

CRSP, on shaded outcrop above falls, 1986, *Schofield 87751* (UBC); on moist sandstone bluff in redwood forest on Zayante Road near Summit Road, 1995, 160 m, *Norris 86869* (UC); on bark of *Torreya californica* near Scott Creek in Swanton, 1997, 25 m, *KMK 410* (CAS); on sandstone boulder in bed of Big Creek 2 m above water line, 2001, 235 m, *KMK 1897* (CAS).

Blindia acuta (Hedw.) B.S.G.

Occasional; on moist rocks. Sporophytes unknown from county.

On wet rocks near Eagle Rock, off Empire Grade, Bonny Doon, 2000, 740 m, *KMK 884* (CAS); on shaded sandstone rocks in Jamison Creek northwest of Boulder Creek (the two collections are about ½ mile apart), 2001, 300 m, *KMK 1271, 1539* (CAS). Reported by Thompson and Ketledge (1958) from rocks in Opal Creek, BBRSP, but I was unable to find it there.

* *Brachythecium albicans* (Hedw.) B.S.G.

Occasional; a weed in irrigated lawns and gardens. Sporophytes unknown from county.

In irrigated garden in Scotts Valley, 2000, 175 m, *KMK 1189* (CAS); a lawn weed in Felton, 2001 85 m, *KMK 1284* (CAS).

Brachythecium asperrimum (Mitt. ex Müll. Hal.) Sull.

Occasional; Usually on wet soil or rocks. Sporophytes unknown from county.

BBRSP, no further data given, *Schofield 6357* (CAN); FC, on granite rock at confluence of north and south forks of Fall Creek, 1999, 175 m, *KMK 658* (CAS); on granite rock at edge of falls in Big Creek at confluence with Boyers Creek, 2001, 285 m, *KMK 1918* (CAS).

* *Brachythecium bolanderi* (Lesq.) Jaeg.

Occasional; on soil or rock in mesic areas, usually shaded or diffusely lit. Sporophytes unknown from county.

QHR, on soil beneath *Quercus* and *Baccharis,* 1996, 145 m, *KMK 280* (CAS); FC, on marble rock of Blue Cliff limestone quarry, 1999, 245 m, *KMK 661* (CAS); on moist soil bank in redwood forest near Rodeo Gulch Road ca 0.5 miles north of Soquel Drive, 2001, 45 m, *KMK 2066* (CAS).

* *Brachythecium frigidum* (C. Müll) Besch.

Common; on splashed rocks or dripping soil in diffuse light. Sporophytes occasional.

FC, on water splashed rock at junction of north and south forks of Fall Creek, 1999, 175 m, *KMK 672* (CAS); FC, on dripping rocks in Ringtail Creek upstream of Fel-

ton-Empire Rd., 1999, 425 m, *KMK 803* (CAS); on sandstone bank of San Lorenzo River upstream of Mill Street Dam in Ben Lomond. This location is submerged under ca 1.5 m of water during summer when the dam is erected, 2001, 90 m, *KMK 1484* (CAS); LL, on sandstone rock in bed of Newell Creek just downstream of Loch Lomond dam, 2001, 120 m, *KMK 1534* (CAS).

* *Brachythecium rutabulum* (Hedw.) B.S.G.

Rare; a lawn weed. Sporophytes unknown from county.

A lawn weed behind San Lorenzo Valley Elementary School, 2000, 105 m, *KMK 1242* (CAS).

* *Brachythecium starkei* (Brid.) B. S. G. var. *pacificum* Lawt.

Rare; submerged in small waterfall. Sporophytes unknown from county.

Submerged in small waterfall in drainage channel along Bay Street in Santa Cruz, 2001, 60 m, *KMK 1830,* (CAS). Note: although this is an odd habitat for this species, the plant fits the description in Lawton (1971) beautifully. The costa dies at the base of the acumen, the leaf tips are twisted, and both stem and branch leaf outlines match her drawings.

* *Brachythecium velutinum* (Hedw.) B.S.G.

Common; on rock, soil or rotting wood usually near water. Sporophytes occasional.

On sandstone bank of San Lorenzo River upstream of Mill Street Dam in Ben Lomond. This site is submerged during summer when the dam is erected, 2000, 90 m, *KMK 1249* (CAS); QHR, on soil immediately above water level in *Salix* swamp near parking lot, 1996, 155 m, *KMK 128* (CAS); HCRSP, on base of *Quercus* ca 0.3 m above water line of Eagle Creek near Graham Hill Road, 1998, 185 m, *KMK 573* (UC); FC, on granite rock in bed of seasonal side channel of Fall Creek, 1999, 250 m, *KMK 673* (CAS).

** *Bruchia flexuosa* (Schwägr.) C. Müll.

Rare; on moist soil in grassland. Sporophytes present on all collections.

UCSC—upper campus, on moist soil in grassland off Empire Grade near mile marker 13.0, 2001, 365 m, *KMK 1456* (CAS); UCSC—upper campus, on moist soil in grassland off Empire Grade near mile marker 12.5, 2001, 365 m, *KMK 1463* (CAS); on wet soil of drainage ditch in Scotts Valley Sky Park, 2003, 160 m, *KMK 2805* (CAS).

Bryolawtonia vancouveriensis (Kindb.) Norris & Enroth

Common at the base of trees in redwood forests, on rock in mixed forest, sometimes near waterline of creeks. Sporophytes occasional.

FC, on base of *Umbellularia* in redwood forest near Fall Creek, 1990, 150 m, *Whittemore 3477* (CAS); HCRSP, on sedimentary rock in temporary drainage gully in redwood forest of Rincon Gorge, 1997, 45 m, *KMK 369* (CAS); WRSP, 2 m up trunk of *Quercus* in mixed forest, 2002, 120 m, *KMK 2580* (CAS).

Bryum argenteum Hedw.

Common in urban areas in cracks in pavement, openings in grassland, also on dry rocks in chaparral. Sporophytes occasional.

Moist sandstone outcrop north of Boulder Creek, 1980, 180 m, *Norris 55559* (UC); sunny irrigated crack in pavement in Capitola, 2000, 30 m, *KMK 1037* (CAS); sunny edge of compacted gravel path in Scotts Valley, 2000, 150 m, *KMK 1121* (CAS); north of Boulder Creek, 1954, 240 m, *Thomas 3718* (CAS); on soil at the base of tree in San

Lorenzo Park in Santa Cruz, 2000, 6 m, *KMK 968* (CAS); BBRSP, on sandstone outcrop in opening in chaparral, 2001, 575 m, *KMK 1310* (CAS).

Bryum barnesii Wood.

Common; on soil in disturbed areas, cracks in pavement, irrigated gardens, beach-side cliffs. Sporophytes rare.

HCRSP, on vernally wet soil near railroad tracks, 1999, 90 m, *KMK 615* (CAS); on seeping sandstone cliff at edge of Capitola beach, 2000, 2–3 m, *KMK 1195* (CAS); RDO, on moist soil at the bottom of a drainage ditch near the beach, 2000, 4 m, *KMK 1218* (CAS); BBRSP, on soil in openings in chaparral near Hwy 236 and China Grade, 2001, 685 m, *KMK 1297* (UC).

* *Bryum bicolor* Dicks.

Occasional; on disturbed soil. Sporophytes unknown from county.

FNMSP, on sandy soil of stranded island in Aptos Creek, 2001, 250 m, *KMK 2040* (CAS); on soil in cracks in pavement in Santa Cruz, 2002, 5 m, *KMK 2556* (CAS); At base of *Bacharris* in grassland east of Watsonville, 2002, 160 m, *KMK 2279* (CAS).

** *Bryum calobryoides* Spence

Rare; on sandstone. Sporophytes unknown from county.

On sandstone outcrop in chaparral at the intersection of Highway 17 and Laurel Rd., 2003, 375 m, *KMK 2653* (CAS) [determined by Spence]

Note: Per Spence (1986) this is an alpine moss. This collection significantly increases the altitudinal range of the species, and may be the current southern limit of the species.

* *Bryum canariense* Brid.

Occasional; on leaf litter in forested areas, sandy soil. Sporophytes rare.

HCRSP, on railroad tie retaining wall, 1996, 120 m, *KMK 581* (CAS); WRSP, on moist leaf litter in redwood forest, 2000, 210 m, *KMK 996* (CAS).

* *Bryum gemmiferum* Wilcz. & Dem.

Rare; on soil in irrigated commercial planting. Sporophytes unknown in county.

On soil at the base of tree in irrigated garden in Scotts Valley, 2000, 175 m, *KMK 1178* (CAS).

* *Bryum gemmilucens* Wilcz. & Dem.

Common; on disturbed soil. Sporophytes occasional.

On damp soil of dirt road around Harkins Slough near Watsonville, 2001, 5 m, *KMK 1286* (CAS); on saturated soil in meadow north of Scotts Valley, 2001, 230 m, *KMK 1326* (CAS); QHR, on bare soil in grassland, 2001, 170 m, *KMK 1336* (UC); on mineral soil in road through pasture in Felton, 2002, 100 m, *KMK 2111* (CAS).

* *Bryum gemmiparum* De Not.

Common; on rocks that are seasonally wet or at stream edges. Sporophytes unknown from county.

HCRSP, on rock at edge of San Lorenzo River, 1999, 25 m, *KMK 611* (CAS); on rock in Boulder Creek, 2000, 200 m, *KMK 982* (CAS); on seasonally wet sandstone rock immediately south of the Eagle Rock lookout tower, 2000, 750 m, *KMK 888* (CAS); on sandstone rock in the San Lorenzo River upstream of the Mill Street dam in Ben Lomond, 2001, 90 m, *KMK 1475* (CAS); RDO, on mudstone rock in seasonal drainage gully onto Waddell beach, 2003, 2 m, *KMK 2646* (CAS).

Note: Bulbils are locally rare in this species but they are present in *KMK 2646.*

* *Bryum laevifilum* Sayed

Rare; on tree bark. Sporophytes unknown from the county.

On bark of *Quercus wislizeni* off Highway 17 at Laurel Rd., 2003, 370 m, *KMK 2702* (CAS) [Confirmed by Spence].

Note: Both Nyholm (1993) and Smith (1978) treat this species as a depauperate *B. flaccidum*. Whether or not this is true, this specimen clearly falls within the *laevifilum* end of the spectrum. This specimen is also remarkable in that the gemmae are so abundant that they obscure large portions of the plants. I have accepted this taxon only because of the presence of the filamentous gemmae. There are numerous collections of small *Rosulabryum capillare* with various combinations of twist to the dried leaves, even within the same collection, and I do not trust naming them either *B. flaccidum* or *B. laevifilum*.

* *Bryum lisae* De Not.

Rare; on soil or soil over rock. Sporophytes on both collections.

FNMSP, on soil over rock in forest, 1999, 780 m, *KMK 725* (CAS); LL, on sheltered soil at high water line of reservoir, 2000, 180 m, *KMK 1058* (CAS).

* *Bryum miniatum* Lesq.

Rare; on seasonally wet rocks. Sporophytes unknown from county.

KMK 327, 1997, on sandstone outcrop in meadow north of Boulder Creek, 240 m, (CAS); *KMK 694,* 1999, BBRSP, on sandstone outcrops in meadow near Sempervirens Falls, 365 m, (CAS).

* *Bryum pseudotriquetrum* (Hedw.) Gaertn. et al.

Common; on soil or soil over rock in at least vernally wet places. Sporophytes occasional.

QHR, on moist sandy loam in shade, 1996, 150 m, *KMK 214a* (CAS); HCRSP, on shaded rocks in forest, 1999, 90 m, *KMK 617* (CAS); on vernally wet rocks north of Scotts Valley, 1999, 240 m, *KMK 709* (CAS); among grasses of disturbed roadside soil, 2000, 395 m, *KMK 962* (CAS).

* *Bryum pyriferum* Crundw. & H. Whiteh.

Occasional; on wet soils. Sporophytes rare.

FNMSP, on stranded soil in the bed of Aptos Creek, 2001, 250 m, *KMK 2041* (CAS) [confirmed by Spence]; WRSP, on rotten log at the margin of a pond on Baldwin Creek, 2002, 195 m, *KMK 2583* (CAS); on moist rock of roadside cut on Little Basin Road near Big Basin, 2000, 440 m, *KMK 1021*(CAS).

* *Bryum subapiculatum* Hampe

Occasional; on soil in disturbed sites. Sporophytes on one collection.

HCRSP, on soil near railroad tracks, 2001, 1999, 90 m, *KMK 616* (CAS) [determined by Spence]; on sandy soil of steep roadside cut near Felton, 120 m, *KMK 1318* (CAS); on thin soil over mudstone in opening in coastal scrub near Yellow Bank Creek, 2002, 50 m, *KMK 2090* (CAS).

* *Bryum violaceum* Crundw. & Nyh.

Rare; on soil in disturbed areas. Sporophytes unknown from county.

On bulldozed pile of soil off road in Bonny Doon, 1999, 580 m, *KMK 917* (CAS).

* *Calliergonella cuspidata* (Hedw.) Loeske

Rare; on soil of creek bank. Sporophytes unknown from county.

On moist shaded soil of drainage creek bank in median of Bay Street, Santa Cruz, 2001, 70 m, *KMK 1826* (CAS).

* *Campylopus subulatus* Schimp. in Rabenh.

Rare; the site was once an extensive freshwater marsh. Sporophytes unknown from county.

On sunny banks of waterway in a trailer park in Scotts Valley, 2000, 150 m, *KMK 1123* (CAS).

Ceratodon purpureus (Hedw.) Brid.

Very common; on poor soils and in disturbed sites that are dry in the summer. Sporophytes common.

On sandy roadside bank near Felton, 1950, *Howell 306a* (CAS); BBRSP, sandstone roadside bank, 1969, 610 m, *Whittemore 3295* (CAS); HCRSP, on concrete lined drainage ditch, 1999, 85 m, *KMK 626* (CAS); QHR, on concrete in grassland, 1996, 130 m, *KMK 206* (CAS).

Ceratodon stenocarpus Bruch & Schimp. ex Müll Hal.

Rare; on poor soil. Sporophytes on both collections.

On sandy road cut above Mount Hermon Road near Felton, 2003, 140 m, *KMK 2803* (CAS); on sandy soil along Soquel-San Jose Road north of Soquel, 2003, 260 m, *KMK 2834* (CAS).

* *Chenia leptophylla* (C. Müll.) Zander

Rare; found only once on moist soil in the middle of a forest trail. Sporophytes unknown from county.

On moist bare soil of fire road near Highway 1 south of Davenport, 1999, 15 m, *KMK 755* (CAS).

Claopodium whippleanum (Sull.) Ren. & Card.

Abundant; on soil and rock banks in diffuse light along trails and roads. Sporophytes rare.

FC, "along Fall Creek", 1961, 180 m, *Thomas 8938* (CAS); FNMSP, on moist soil in redwood forest, 1980, *Norris 55642* (UC); QHR, on mudstone in mixed evergreen forest, 1996, 200 m, *KMK 191* (CAS); BBRSP, on shaded sandstone drainage gully in chaparral, 2001, 550 m, *KMK 1311* (UC); HCRSP, on trailside bank in coast redwood forest, 2002, 130 m, *KMK 2272* (CAS).

* *Crossidium aberrans* Holz. & Bartr.

Rare, thus far found only on sandstone near Scotts Valley. Sporophytes on this collection.

On exposed sandstone outcrop in grassland near Scotts Valley High School, 2001, 250 m, *KMK 1351* (CAS).

* *Crossidium squamiferum* (Viv.) Jur.

Rare, thus far found only on sandstone rock in chaparral. Sporophytes on this collection.

On exposed sandstone outcrop in chaparral near Eagle Rock, 2001, 690 m, *KMK 1339* (CAS).

* *Crumia latifolia* (Kindb.) Schof.

Occasional; on wet rocks from seeping calcareous walls or permanently submerged in creeks. Sporophytes unknown from county.

BBRSP, on rocks in San Lorenzo River submerged in winter, 1999, 30 m, *KMK 674* (CAS); on roadside calcareous seep north of Corralitos, 1999, 500 m, *KMK 714* (CAS); permanently submerged in chute type cascade of Kings Creek north of Boulder Creek, 280 m, *KMK 1025* (CAS).

Dendroalsia abietina (Hook.) Britt.

Abundant; on the bark of trees, usually hardwood, occasionally on rock. Sporophytes common.

CRSP, common on trunks of *Quercus,* 1986, *Schofield 87567* (UBC); QHR, common on trunks of *Quercus agrifolia,* 1996, 200 m, *KMK 113* (CAS); FC, on trunk of *Quercus* near the parking area, 1997, 170 m, *KMK 423*

(CAS); on *Quercus* bark in redwood forest UCSC campus, 1980, 215 m, *Norris 55660* (UC); BBRSP, on sandstone rock in mixed evergreen forest above Pine Mountain trail, 2002, 490 m, *KMK 2510* (CAS); CRSP, abundant on sandstone rocks near Castle Rock, 2002, 975 m, *KMK 2560* (CAS).

Dichodontium pellucidum (Hedw.) Schimp.
Common; on rocks in creek and river banks that are seasonally submerged. Sporophytes unknown from county.
FNMSP, on boulder along stream, 1992, 90 m, *Whittemore 4032* (CAS); FC, on granite rocks at edge of North Fork Fall Creek, 1997, 300 m, *KMK 438* (CAS); BBRSP, on sedimentary rock in bed of Opal Creek, 2000, 390 m, *KMK 974* (CAS); on irrigated garden soil Capitola, 2000, 30 m, *KMK 1052* (CAS).

Dicranella heteromalla (Hedw.) Schimp.
Occasional; On moist soil banks in redwood forest. Sporophytes seen once.
On decayed rock of roadside bank between Felton and Ben Lomond, 1965, *Schofield & Thomas 26418* (UBC); BBRSP, on soil of roadside bank near Waddell Creek in redwood forest, 1999, 25 m, *KMK 782* (CAS); on moist mineral soil bank near Little Creek in Swanton, 2001, 70 m, *KMK 1892* (CAS).

Dicranella howei Ren. & Card.
Common; on moist soil near water. Sporophytes seen twice.
FNMSP, on rocks in Aptos Creek, 1997, 150 m, *KMK 378* (CAS); HCRSP, on moist soil over mudstone on banks of Eagle Creek, 1999, 150 m, *KMK 631* (CAS); BBRSP, on soil of shaded slope in redwood forest, 1956, *Schofield 6457* (UBC); WRSP, on soil bank near reservoir off Englesman Loop trail, 2002, 75 m, *KMK 2247* (CAS).

Dicranoweisia cirrata (Hedw.) Lindb. in Milde
Very common; on dead wood, on the bases of conifers or chaparral shrubs. Sporophytes common.
On charred redwood stump near Felton, 1949, *Howell 297* (CAS); QHR, on burnt redwood stump, 1996, 260 m, *KMK 220* (CAS); FC, on bark of fallen *Pseudotsuga*, 1997, 300 m, *KMK 441* (CAS); WRSP, on dead wood in chaparral, 2000, 210 m, *KMK 941* (CAS).

* *Dicranum fuscescens* Turn.
Rare; on bark of standing and fallen trees. Locally common in the West Waddell Creek watershed. Sporophytes unknown from county.
BBRSP, on bark of *Pseudotsuga* near headquarters of BBRSP, 2000, 300 m, *KMK 1004* (CAS); BBRSP, on bark of redwood tree fallen across West Waddell Creek, 2002, 160 m, *KMK 2479* (CAS).

* *Dicranum howellii* Ren. & Card.
Rare; thus far found only on wet rotting wood in a pond in redwood forest. Sporophytes unknown from county.
FNMSP, on wet rotting wood in White's Lagoon, 1999, 430 m, *KMK 774* (CAS).

Dicranum tauricum Sapeh.
[*Orthodicranum tauricum* (Sapeh) Smirnova]
Common; on bark of coast redwood or Douglas fir, alive or dead. Sporophytes unknown from county.
FC, on rotten log along Fall Creek, 1961, 180 m, *Thomas 8956* (CAS); on bark of fallen redwood tree, 1997, 230 m, *KMK 353* (CAS); BBRSP, on bark of coast redwood tree, 2000, 350 m, *KMK 978* (CAS).

Didymodon brachyphyllus (Sull.) Zander
Common on Purisma Formation sandstone in the center of the county, rare elsewhere. Sporophytes unknown from county.
On sandstone bedrock in grassland above Scotts Valley High School, 2001, 250 m, *KMK 1329* (CAS); On Purisma sandstone rock in open chaparral at peak of Rodeo Gulch Rd., 2001, 265 m, *KMK 2069, 2070* (CAS); On Purisma sandstone road bank in *Quercus-Eucalyptus* forest, 2002, 30 m, *KMK 2290* (CAS); BBRSP, near upper entrance to park, 1951, *Steere s.n.* (BUF) (cited in Zander and Ochyra 2001).

Didymodon insulanus (De Not.) M. Hill
[*Didymodon vinealis var. flaccidus* (Bruch & Schimp. in Schimp.) Zander]
Abundant; on wet or dry road side and trailside banks, concrete, or occasionally on trees. Sporophytes very common.
RDO, on shaded road bank through redwood forest near Waddell Creek, 1961, 30 m, *Thomas 9235* (CAS); FNMSP, on soil bank near Aptos Creek, 1992, 100 m, *Whittemore 4035* (CAS); QHR, on broken concrete below the pond, 1996, 45 m, *KMK 202* (CAS); HCRSP, on redwood bark in Rincon Gorge, 1997, 45 m, *KMK 363* (CAS); One meter up the trunk of *Pseudotsuga* tree behind San Lorenzo Elementary School near Felton, 2000, 100 m, *KMK 1211* (CAS).
Note: After examining all of my collections of *Didymodon*, I have come to agree with Zander (1981) that the *D. vinealis–D. rigidulus* group is an impossible continuum of combinations of characteristics with the commonly accepted species being only waypoints along that continuum. One has to decide whether to include all of the taxa as varieties, as Zander did in 1981, or separate them out into species, as Zander has done in subsequent publications on this genus (Zander 1999, 2001). I have chosen to maintain them all as species. This taxon is easily as differentiated from *D. vinealis* as any of the other taxa in that group. The leaf shape is very long lanceolate, and recurvature of the margins is limited to the lower ⅓ of the leaf. All the members of the *D. vinealis* group are connected by intermediate forms, and if any are separated into different species, this one ought to be also. *KMK 1211* is especially interesting. It is recurved only in the proximal ¼, with the remaining margin bistratose with a stair-step type dentition that is reminiscent of *Amphidium californicum*. This seems to be a midway point on the continuum between the newly described *D. eckeliae* (Zander 2001) and the other specimens of *D. vinealis* with bistratose margins.

Didymodon nicholsonii Culm.
Common, on dry rock or concrete. Sporophytes common.
CRSP, On dry sandstone in chaparral, 1999, 860 m, *KMK 665* (CAS); HCRSP, on concrete wall of drainage ditch in full sun, 1999, 85 m, *KMK 627* (CAS); BBRSP, on dry sandstone outcrop in chaparral, 2001, 680 m, *KMK 1291* (CAS); on dry limestone rock in coast redwood forest near Laguna Creek, 2001, 215 m, *KMK 1522* (CAS).
Note: There are several collections that are entirely bistratose in the distal ⅓ [*KMK 665, 879, 1281* (CAS)]. Sharp leaf channelization and conical apical cell, along with lack of a subulate apex, keeps these latter plants from inclusion in *D. rigidulus*. On advice from Zander (personal communication) I have included them in *D. nicholsonii*.

* *Didymodon norrisii* Zand.

Rare; on seasonally wet rock in full sun. Sporophytes unknown from county.

On sandstone rock in seasonal drainage near Eagle Rock lookout tower, 2000, 740 m, *KMK 890* (CAS).

Didymodon rigidulus Hedw.

Occasional; on dry or moist rock or concrete. Sporophytes common.

NBSB, on moist sandstone of weeping coastal cliff, 1997, 2 m, *KMK 563* (CAS); HCRSP, on rocks in winter flood zone of the San Lorenzo River, 1999, 30 m, *KMK 612* (CAS); on dry concrete buttress forming the end of Mill Street Dam in Ben Lomond, 2001, 90 m, *KMK 1468* (CAS).

* *Didymodon tophaceus* (Brid.) Lisa

Rare; on irrigated soil near stucco building. Sporophytes unknown from county.

On moist soil of irrigated planting bed near DMV building in Capitola, 2000, 30 m, *KMK 1048* (CAS).

Didymodon vinealis (Brid.) Zander

Very common; on concrete, rock, rarely on trees. Sporophytes very common.

BBRSP, on moist sandstone near upper entrance, 1951, *Steere s.n.* (UBC, NY); WRSP, on shaded soil bank above reservoir, 1999, 80 m, *KMK1090* (CAS); UCSC, on crevice on marble boulder opposite the Barn Theater, 2002, 90 m, *KMK 2127* (CAS); LL, on splashed steel catch basin below the dam, 2001, 190 m, *KMK 1514* (CAS).

Note: I have several collections with bistratose margins [see *KMK 1090* (CAS)]. The leaves are too narrow for inclusion in *D. nicholsonii*.

Ditrichum ambiguum Best.

Common; on sandstone road and trail banks in open forests. Sporophytes common.

On soil in redwood forest near Bonny Doon, 1993, 480 m, *Whittemore 4432* (CAS); QHR, on mudstone gravel in mixed evergreen forest, 1996, 210 m, *KMK 188* (CAS); HCRSP, on sandy soil in chaparral, 1999, 180 m, *KMK 640* (CAS); roadside bank in mixed evergreen forest, 1999, 730 m, *KMK 713* (CAS).

Ditrichum schimperi (Lesq.) Kuntze

Common; on soil in various habitats. Sporophytes common.

BBRSP, along trail near Sempervirens Falls, 1947, *Koch 2063* (UC); FC, on soil in chaparral, 1999, 490m, *KMK 595* (CAS); trailside bank above Liddell Creek in redwood forest, 1999, 75 m, *KMK 756* (CAS).

* *Drepanocladus aduncus* (Hedw.) Warnst.

Occasional; a weed in irrigated gardens. Sporophytes unknown from county.

On shaded soil under shrubs in irrigated planter bed in Capitola, 2000, 30 m, *KMK 1051* (CAS); on wet soil of bank of Willow Pond in Scotts Valley, 2000, 150 m, *KMK 1120* (CAS); on soil of irrigated planting area in Scotts Valley, 2000, 175 m, *KMK 1184* (CAS).

* *Entosthodon attenuatus* (Dicks.) Bryhn

Rare; on moist soil in grassland, found near Bonny Doon. Sporophytes in both collections.

UCSC—upper campus, on moist soil in grassland, 2001, 360 m, *KMK 1457* (CAS); UCSC—upper campus, on moist soil in grassland, 2001, 350 m, *KMK 1461* (CAS). The two collections are about one km apart.

Ephemerum serratum (Schreber ex Hedw.) Hampe

Common in winter; on disturbed, moist soil. Sporophytes always present.

QHR, on open soil in shade of *Quercus,* 1997, 150 m, *KMK 315* (CAS); HCRSP, on bare soil in openings in meadow near entry kiosk to park, 1999, 90 m, *KMK 623* (CAS); on moist soil in redwood forest with scattered meadows on UCSC campus, 1980, 215 m, *Norris 55679* (UC).

Epipterygium tozeri (Grev.) Lindb.

Common; on moist soil in openings in forest, or trail banks. Often a pioneer on eroded mineral soil banks. Sporophytes occasional.

On crumbly soil in redwood forest near Bonny Doon, 1993, 490 m, *Whittemore 4434* (CAS); FNMSP, moist soil of road bank in redwood forest, 1980, *Norris 55636* (UC); Glenwood, 1893, *Michener & Bioletti s.n.* (UC); QHR, at foot of gravelly slide in redwood forest, 1996, 180 m, *KMK 189* (CAS).

Eucladium verticillatum (Hedw.) Bruch. & Schimp. In B.S.G.

Common; usually on moist calcareous soil or rocks. Sporophytes occasional.

BBRSP, On wet soil in redwood forest near Opal Creek, 2000, 275 m, *KMK 1010* (CAS); FC, on dripping calcareous rocks in Ringtail Creek above Felton Empire Road, 1999, 425 m, *KMK 802* (CAS); on wet calcareous clay wall above Hinckley Creek near Soquel Creek, 1999, 115 m, *KMK 690* (UC).

** *Eurhynchium hians* (Hedw.) Sande-Lac.

Rare; aquatic. Sporophytes unknown from county.

WRSP, on roots of coast redwood tree that form a cascading dam on Baldwin Creek, 2002, 85 m, *KMK 2581* (CAS).

Note: Although this species is not normally submerged, the plant fits very well with the description of *E. hians* given in Crum and Anderson (1981). The leaves are far too acuminate for *Platyhypnidium riparioides,* and the costa is not strong enough for *E. pringlei* and too strong for *E. subrusciforme.* The collection was made in September before the winter rains began, making it extremely probable that these plants are submerged year-round.

Eurhynchium oreganum (Sull.) Jaeger
[*Kindbergia oregana* (Sull.) Ochyra]

Common; on soil and leaf litter in forests. Sporophytes occasional.

BBRSP, on ground, 1970, *Franck s.n.* (UC); FNMSP, on soil in 2nd growth redwood forest, 1980, *Norris 55627* (UC); QHR, on trail bank in redwood forest on Sunset Trail, 1996, 250 m, *KMK 234* (CAS); HCRSP, on leaf litter in small meadow on Ox Trail, 1999, 160 m, *KMK 654* (UC); FC, on sunny seeping wall above North Fork Fall Creek, 1999, 245 m, *KMK 692* (CAS).

Eurhyrinchium praelongum (Hedw.) Schimp. in B. S. G.
[*Kindbergia praelonga* (Hedw.) Ochyra]

Abundant; along the banks of waterways, as an irrigated lawn weed or along dryer trails in forest. It could almost be said that every waterway in Santa Cruz County has this moss. Sporophytes rare.

On shaded log in redwood forest, 1949, *Howell 290* (CAS); FNMSP, on moist log in redwood forest, 1980, *Norris 55629* (UC); QHR, on walls of Quail Hollow Creek in shade, 1996, 145 m, *KMK 199* (CAS); HCRSP, on banks of small unnamed creek emptying into San Lorenzo River just upstream of "Garden of Eden", 1996, 75

m, *KMK 216* (CAS); BBRSP, common on rocks along Opal Creek, 2000, 400 m, *KMK 975* (CAS).

* *Fabronia pusilla* Raddi

Occasional; on bark of hardwood trees with rough bark, rarely on rock. Sporophytes common.

On bark of *Quercus wislizenii* in Bonny Doon, 2000, 580 m, *KMK 861* (CAS); on bark of *Juglans hindsii* roadside near Ben Lomond, 2001, 100 m, *KMK 1324* (CAS); on bark of *Quercus lobata* in front of San Lorenzo Valley Elementary School, 2001, 95 m, *KMK 1925* (CAS); on under hang of sandstone rock on Zayante Road near Summit Road, 2002, 555 m, *KMK 2585* (CAS).

Fissidens bryoides Hedw.

Very common; on wet soil or rocks, usually shaded. Sporophytes occasional.

BBRSP, on soil bank, 1970, *Frank s.n.* (UC); FNMSP, moist soil of road bank in redwood forest, 1980, *Norris 55620* (UC); FC, saturated soil of trail side spring above North Fork Fall Creek, 1997, 240 m, *KMK 437* (CAS); on moist shaded soil above Arana Gulch Santa Cruz, 2000, 7 m, *KMK 1055* (CAS); on moist, shaded granite wall above Laguna Creek, 2001, 230 m, *KMK 1492* (CAS).

Fissidens crispus Mont.

Very common; on moist shaded soil of creek, trail, and road banks. Sporophytes occasional.

On soil in drainage channel in redwood forest north of Boulder Creek, 1954, 550 m, *Thomas 3667* (CAS); FNMSP, shaded bank near Aptos Creek, 1992, 120 m, *Whittemore 4052* (CAS); QHR, on moist sandy loam under *Quercus*, 1996, 150 m, *KMK 213* (CAS); submerged on rocks in Liddell Creek near Davenport, confirmed as this species by Pursell, this population was truly aquatic in this year round stream, 14 Aug 1999, 50 m, *KMK 753* (CAS).

Note: in the recent past, *Fissidens limbatus* Sull. was often misapplied to this plant.

Fissidens curvatus Hornsch.

Very common; on moist, bare soil in meadows or open forests. Abundant in edges of grassland and coastal scrub north of Scotts Creek and at UCSC. Sporophytes common.

On moist soil in redwood forest UCSC campus, 1980, 210 m, *Norris 55656* (UC); HCRSP, on soil in openings in grassland near main entrance in Felton, 1999, 90 m, *KMK 620* (CAS); WRSP, on shaded bare soil near Wilder Creek, 1999, 45 m, *KMK 819* (CAS).

* *Fissidens fontanus* (B. Pyl.) Steud.

Rare; margin of a pond. Sporophytes unknown from county.

QHR, on concrete dam of Quail Hollow Pond, 2002, 150 m, *KMK 2613* CAS.

Fissidens grandifrons Brid.

Common; on water splashed rocks of creeks and waterfalls, usually, but not always calcareous. Sporophytes unknown from county.

FC, on rock in waterfall at conjunction of North and South Forks of Fall Creek, 1997, 190 m, *KMK 352* (CAS); submerged on rock in East Fork Liddell Creek, 1999, 50 m, *KMK 750* (UC); on dripping sandstone wall above Boulder Creek, 2000, 210 m, *KMK 985* (CAS); on dripping limestone wall above Laguna Creek, 2001, 215 m, *KMK 1495* (CAS).

Fissidens pauperculus Howe

Rare; on soil in coast redwood forest. Sporophytes unknown from county.

BBRSP, 1949, cited with no further data in Koch (1950), *Koch 2207a* (ILL); FNMSP, on bank of Loma Prieta Grade Trail in coast redwood forest, 2002, 110 m, *KMK 2637* (CAS).

* *Fissidens sublimbatus* Grout

Occasional, poor soils that dry in summer, often in grassland. Sporophytes rare.

On sandstone rock outcrop in open chaparral near Rodeo Gulch Road at mile marker 0.56, 2001, 265 m, *KMK 2067* (CAS); UCSC, on bare soil at forest-meadow boundary in Marshall Field, 2001, 350 m, *KMK 1458* (CAS).

*** *Fissidens taylorii* C. Müll.

Rare, on wet soil bank. Sporophytes present on this one collection.

WRSP, on wet soil bank of deep drainage gully in grassland, 2002, 75 m, *KMK 2252* (CAS) [Determined by Pursell]. This is only the second collection of this taxon in North America north of Mexico (Pursell, personal communication) For a description of this moss, and a discussion of its range, see Pursell (1997).

Fissidens ventricosus Lesq.

Occasional; on submerged rocks in creeks in northern Santa Cruz County. Sporophytes rare.

On submerged rocks in Boulder Creek, 2000, 210 m, *KMK 979* (CAS); BBRSP, on submerged rocks in Opal Creek, 2000, 280 m, *KMK 1011* (CAS); on submerged rocks in San Lorenzo River in Ben Lomond, 2000, 90 m, *KMK 1175* (CAS).

Fontinalis neomexicana Sull. & Lesq.

Cited in Welch (1960). This plant is probably extirpated from Santa Cruz County. It no longer exists in Sempervirens Creek where Koch collected it. A dam has been constructed on that creek since his collection.

BBRSP, Sempervirens Creek near Camp 7, 1947, *Koch 2071* (MICH).

* *Funaria hygrometrica* Hedw.

Very common; on disturbed moist soil. Very common in Capitola near the shore of Monterey Bay. Sporophytes almost always present.

QHR, on sandy soil in trail, 1996, 170 m, *KMK 148* (UC); HCRSP, on soil of Rincon Gorge parking area, 1999, 90 m, *KMK 625* (CAS); on cracks in pavement adjacent to the Capitola Beach, 2000, 7 m, *KMK 1199* (CAS).

* *Funaria muhlenbergii* Turn.
[*Entosthodon muhlenbergii* (Turn.) Fife]

Occasional; on poor soils, tends to inhabit dryer sites than *F. hygrometrica*. Sporophytes common.

FC, on soil over rock on Blue Cliff, 1999, 245 m, *KMK 663* (CAS); on bare soil in lawn in Harvey West Park Santa Cruz, 2001, 20 m, *KMK 1240* (CAS).

* *Grimmia laevigata* (Brid.) Brid.

Occasional; on higher elevation sandstone outcrops in northern Santa Cruz County. Sporophytes occasional.

BBRSP, on sandstone rock along China Grade Rd, 1999, 685 m, *KMK 706* (CAS); on sandstone rock in pasture near Eagle Rock, 2000, 650 m, *KMK 873* (CAS).

* *Grimmia lisae* De Not.

Common; on seasonally wet rocks, or shaded rocks in the forest. Sporophytes uncommon.

HCRSP, on rocks 2 m above water line of San Lorenzo

River, 1997, 90 m, *KMK 444* (CAS); HCRSP, on dry rocks in oak forest high above San Lorenzo River, 1999, 120 m, *KMK 602* (CAS); on granite rock in Boulder Creek ca 1 m above water line, 2000, 200 m, *KMK 1002* (CAS).

* *Grimmia montana* B. S. G.

Occasional; on dry sandstone rock, around the Ben Lomond Sandhills. Sporophytes occasional.

BDEP, forming cushions on dry sandstone in chaparral, 1999, 520 m, *KMK 760* (CAS); QHR, on south facing sandstone rock, 2000, 200 m, *KMK 937* (CAS); QHR, forming cushions on dry sandstone, 2000, 175 m, *KMK 1142* (CAS).

** *Grimmia ovalis* (Hedw.) Lindb.

Occasional; found only in extreme northern Santa Cruz County. Sporophytes unknown in county.

BBRSP, on shaded sandstone boulder near China Grade, 1999, 685 m, *KMK 723* (CAS) [determined by Muñoz]; BBRSP, on sunny sandstone knob in chaparral near China Grade, 2001, 685 m, *KMK 1293* (CAS); on sunny sandstone rock near Eagle Rock, 2000, 730 m, *KMK 906* (CAS) [determined by Muñoz].

Grimmia pulvinata (Hedw.) Sm.

Common; on concrete or dry calcareous rocks. Sporophytes very common.

FC, on limestone boulder, 1965, *Schofield & Thomas 26452* (UBC); CRSP, on roadside shale Highway 9 just south of summit, 1999, 745 m, *KMK 666* (CAS); BBRSP, on sunny concrete near radio tower at the west end of Chalks Ridge, 2000, 470 m, *KMK 1079* (MA) [determined by Muñoz].

Grimmia trichophylla Grev.

Very common; the most common *Grimmia* in the county. On dry rocks in a variety of habitats. Sporophytes common.

On rock in redwood forest along Ice Cream Grade in Bonny Doon, 1993, 490 m, *Whittemore 4440* (CAS); QHR, on dry sandstone shaded by oaks, 1997, 170 m, *KMK 403* (CAS) [determined by Muñoz]; FC, on dry granite rock under *Lithocarpus,* 1997, 245 m, *KMK 434* (CAS); BBRSP, on sandstone in chaparral near China Grade, 2001, 680 m, *KMK 1292* (CAS).

Note: gemmae are rare on this species in Santa Cruz county.

* *Grimmia ungeri* Jur.

Rare; thus far found only on Santa Margarita Sandstone. Sporophytes unknown from county.

QHR, on sandy soil in low mounds in full sun, 1996, 185 m, KMK 120 (CAS) [determined by Muñoz]; QHR, on sandstone boulders, 1996, 170 m, *KMK 121* (UC, MA) [determined by Muñoz].

Gymnostomum aeruginosum Sm.

Common; usually on calcareous rock or soil in diffuse light. Sporophytes unknown from county.

On moist sandstone north of Boulder Creek, 1980, 185 m, *Norris 55584* (UC); Pogonip, on limestone wall, along Spring Trail, 1997, 120 m, *KMK 314* (CAS); BBRSP, on sandstone in chaparral, 2001, 570 m, *KMK 1316* (CAS).

* *Hedwigia stellata* Hedenäs

Occasional; on dry rocks of road cuts or openings in forest at higher elevations. Sporophytes common.

BDEP, on sandstone under *Arctostaphylos,* 1996, 520 m, *KMK 138* (CAS); on roadside sandstone on Santa Rosalita Mountain outside of FNMSP, 1999, 730 m, *KMK 712* (CAS); On rock in pasture south of Eagle Rock, 2001, 660 m, *KMK 1272* (CAS).

* *Hennediella heimii* (Hedw.) Zand.

Occasional; on disturbed soil. Sporophytes common.

On disturbed soil of road through pasture near Yellow Bank Creek, 2002, 25 m, *KMK 2107* (CAS); on disturbed soil of road through pasture in Felton, 2002, 100 m, *KMK 2109* (CAS); WRSP, abundant on trails of first coastal escarpment, 2003, 15 m, *KMK 2686* (CAS).

* *Hennediella stanfordensis* (Steere) Blockeel

Common; on disturbed, open, moist soil. Sporophytes unknown from county.

CRSP, on bare soil of hiking trail off Highway 9 near Hwy 35, 1999, 730 m, *KMK 664* (CAS); on bare moist soil of park ca 100 m from Capitola Beach, 2000, 15 m, *KMK 1197* (CAS); RDO, on moist soil of dirt road in front of "The Brown House", 2000, 10 m, *KMK 1224* (CAS).

Homalothecium arenarium (Lesq.) Lawt.

Common; on rocks or mineral soil near chaparral, or in grasslands. Sporophytes unknown from county.

On thin soil over sandstone near Highway 9 north of Boulder Creek, 1980, 180 m, *Norris 55605* (UC); QHR, on gravelly roadside soil near park entry, 1996, 160 m, *KMK 181* (CAS); RDO, on sandy soil of stabilized dune shaded by *Baccharis* and *Pinus,* 2000, 20 m, *KMK 1221* (CAS); HCRSP, on soil in chaparral under *Arctostaphylos* near Pine Trail, 1999, 185 m, *KMK 636* (CAS); WRSP, on soil of grassy bank near reservoirs, 1999, 70 m, *KMK 839* (CAS).

Homalothecium nuttallii (Wils.) Jaeg.

Abundant; on tree trunks, occasionally on rocks or concrete. Sporophytes occasional.

On bark at base of *Lithocarpus* near Highway 9 north of Boulder Creek, 1980, 180 m, *Norris 55590* (UC); on bark of *Alnus* along Liddell Creek near Highway 1, 1993, 30 m, *Whittemore 4425* (CAS); QHR, on dry concrete culvert, 1997, 130 m, *KMK 281* (CAS); FC, on bark of *Quercus* near parking lot, 1997, 170 m, *KMK 424* (CAS); on bark of *Salix* near Soda Lake, 2000, 45 m, *KMK 914* (CAS).

Homalothecium pinnatifidum (Sull.) Lawt.
[*Homalothecium aureum* (Spruce) H. Robins.]

Common; on soil or rocks in meadows, chaparral, or openings in forest. Sporophytes unknown from county.

On rock outcrops at northern end of Hilton Airport [note: this is now Boulder Creek Golf Course], 1954, 245 m, *Thomas 3675* (CAS); CRSP, on roadside soil bank on Highway 9 at mile marker 26.00, 1999, 780 m, *KMK 677* (CAS); FNMSP, on soil in meadow along trail to Buzzards Lagoon, 1999, 685 m, *KMK 732* (CAS); WRSP, on dead wood in opening in chaparral, 2000, 230 m, *KMK 956* (CAS).

* *Hygrohypnum bestii* (Ren. & Bryhn.) Broth.

Occasional; found only on logs or rock in creeks in uninhabited areas. Sporophytes unknown in county.

FC, on submerged granite rocks at confluence of North and South Forks of Fall Creek, 1999, 175 m, *KMK 798* (CAS); CRSP on splashed sandstone rock at the base of Castle Rock Falls, 2002, 815 m, *KMK 2559* (CAS); on granite rock submerged in Laguna Creek near Smith Grade in Bonny Doon, 2001, 200 m, *KMK 1498* (CAS); in continual splash of waterfall at the confluence of Boyers and Big Creeks, 2001, 285 m, *KMK 1896* (CAS).

Hypnum circinale Hook.

Occasional in BBRSP, not found elsewhere. On bark of

softwood trees both standing and fallen. Sporophytes occasional.

BBRSP, on redwood stumps, 1946, *Richards et al. 1509* (UC); BBRSP, along Sempervirens Creek, 1947, *L.F. Koch 2030a* (UC); BBRSP, On bark of redwood tree near Opal Creek, 2000, 290 m, *KMK 1015* (CAS); BBRSP, on fallen redwood log over West Waddell Creek near Kelly Creek, 2002,160 m, *KMK 2480* (CAS).

* *Hypnum subimponens* Lesq.

Rare; on rock in diffuse light. Sporophytes very common.

FC, on limestone rocks in mixed forest above lime kilns, 1997, 250 m, *KMK 358* (CAS); HCRSP, on granite rocks above San Lorenzo River, 1998, 60 m, *KMK 583* (CAS); on dry granite wall on bank of Big Creek near Davenport, 2001, 120 m, *KMK 1505* (CAS).

Isothecium cristatum (Hampe) Robins.

Abundant; on bases of trees or shrubs in forest and chaparral. Sporophytes common.

FC, abundant on logs and stumps, 1961, *Schofield 12906* (UC); CRSP, at base of trunk of *Pseudotsuga*, 1986, *Schofield 87754* (UBC); QHR, on sandstone rock in chaparral along Italian Trail, 1997, 200 m, *KMK 284* (CAS); HCRSP, on ground in chaparral along Powder Mill Trail, 1998, 185 m, *KMK 588* (CAS).

Isothecium myosuroides Brid.

Abundant; on soil, rock, rotting wood and tree trunks and branches. Sporophytes common.

FC, along Fall Creek, 1961, 180 m, *Thomas 8934,* (CAS); CRSP, as *I. stoloniferum,* outcrop in oak woodland, 1986, *Schofield 87757,* (UBC); FNMSP, on moist log in redwood forest, 1980, *Norris 55645,* (UC); HCRSP, on soil over rock above Eagle Creek, 1998, 70 m, *KMK 579,* (CAS); BBRSP, festooning dead branches of shrubs in redwood forest, 2000, 985 m, *KMK 1019,* (CAS).

Note: This taxon is extremely variable and may well represent several species. Until this group is better understood and published, I will treat it as a single species.

Isothecium obtusatulum Kindb.

Occasional, but probably overlooked; on tree bark or soil near water. Sporophytes unknown from county.

On tree bark near the upper San Lorenzo River off the Saratoga Toll Rd., 2002, 240 m, *KMK 2535* (CAS); HCRSP, on soil over rock near the San Lorenzo River at Eagle Creek, 1998, 60 m, *KMK 579* (CAS); FC, on wooden bridge beam across Fall Creek, 1997, 135 m, *KMK 321a* (CAS).

Leptobryum pyriforme (Hedw.) Wils.

Common; on moist soil or rotting wood. Sporophytes common.

QHR, on moist soil in swamp near parking area, 1996, 155 m, *KMK 244* (CAS); FC, on moist sandstone wall beyond spring above North Fork Fall Creek, 1997, 245 m, *KMK 389* (CAS); on a wet patch of otherwise dry roadside rock along Eureka Canyon Road mile marker 8.68, 1999, 565 m, *KMK 715* (CAS); QHR, on wet soil of receding pond margin, 2002, 150 m, *KMK 2614* (CAS).

Note: *KMK 2614* has abundant rhizoidal tubers.

* *Leptodictyum riparium* (Hedw.) Warnst.

Common; on rotting wood in swampy lagoons, river banks, irrigated lawn weed. Sporophytes common in lagoons.

FNMSP, on branches fallen into the water of Buzzards Lagoon, 1999, 565 m, *KMK 727* (CAS); an irrigated lawn weed in Capitola, 2000, 5 m, *KMK 1057* (CAS); on mud-

stone rock in the bed of San Lorenzo River in the flood zone of Mill Street Dam in Ben Lomond, 2001 90 m, *KMK 1228* (CAS). This site is submerged under 2+ m of water during the summer months when a dam is erected to create a swimming area.

Leucolepis acanthoneura (Schwägr.) Lindb.

Common; on the upper banks of rivers and creeks. Sporophytes occasional.

BBRSP, no further location data available, 1926, *Wiesendanger s.n.* (CAS); FNMSP, on soil bank near stream near George's Campground, 1992, 90 m, *Whittemore 4038* (CAS); HCRSP, on soil in redwood forest in Rincon Gorge, 1997, 45 m, *KMK 362* (UC); on dry granite rock above banks of Big Creek below falls, 2001, 45 m, *KMK 1504* (CAS).

Metaneckera menziesii (Drum.) Steere

Occasional; usually on rock in mixed or redwood forest. Sporophytes unknown from county.

CRSP, on shaded outcrop above falls, 1986, *Schofield 87550* (UBC); FC, on limestone cliff near lime kilns above South Fork, 1997, 260 m, *KMK 356* (UC); WRSP, on sandstone boulder above Baldwin Creek, 2002, 110 m, *KMK 2576* (CAS); on calcareous rock on upper banks of Laguna Creek, 2001, 65 m, *KMK 1862* (CAS).

* *Microbryum davallianum* (Sm.) Zand.

Occasional in 2002, absent in other years; on disturbed calcareous soil. Sporophytes on all collections.

UCSC, on disturbed soil in grassland near entrance to campus, 2002, 105 m, *KMK 2125* (CAS); WRSP, on compacted soil at the edge of Englesman Loop trail in sun, 2002, 65 m, *KMK 2254* (CAS). on bare soil bank in pasture east of Yellow Bank Creek near Highway 1, 2002, 25 m, *KMK 2091* (CAS).

Note: Per Zander (1993), all specimens of *Microbryum* with erostrate opercula and papillose or spiculose spores have been referred to this species.

* *Microbryum starkeanum* (Hedw.) Zand.

Rare; on the north coast grasslands, not found elsewhere. Sporophytes on the only collection.

On bare soil in opening in grassland off Highway 1 north of Davenport, 2002, 125 m, *KMK 2103* (CAS).

Mielichhoferia elongata (Hoppe & Hornsch.) Hornsch

Occasional; on vertical moist soils in redwood forest, or on dry protected sandstone in chaparral. Common on moist cliffs of the immediate coast. Sporophytes common.

Greyhound Rock, on moist crack in salt spray in coastal scrub on seaward cliffs, 1995, sea level, *Norris 86878* (UC); on shaded vertical surfaces of sandstone boulders in chaparral, 1999, 525 m, *KMK 738* (CAS); BBRSP, at the base of a moist road bank in redwood forest near Camp Herbert, 1999, 25 m, *KMK 784* (UC); on moist soil over mudstone on seaward cliff south of Davenport Landing, 2001, 2 m, *KMK 1490* (CAS).

** *Mnium marginatum* (Dicks. ex With.) P. Beauv.

Rare; on wet rocks. Sporophytes unknown from county.

On splashed sandstone rock in Big Creek, 2001, 135 m, *KMK 1500* (CAS).

Neckera douglasii Hook.

Occasional; found on trees mostly in coast redwood forest. Sporophytes occasional.

BBRSP, on redwood stump, 1946, *Richards et al. #1510* (UC); on *Lithocarpus* bark in redwood forest along Highway 9 north of Boulder Creek, 1994, 200 m, *Norris & Piippo 82261* (UC); BBRSP, on *Lithocarpus* bark in red-

wood forest near Opal Creek, 2000, 290 m, *KMK 1008* (CAS); festooning bark of *Alnus* fallen over Laguna Creek, 2001, 90 m, *KMK 1861* (CAS).

Orthodontium gracile (Wils. in Smith & Sowerby) Schwägr. ex B.S.G.

Common; on bark of redwood trees or logs. Sporophytes rare.

FNMSP, on moist log in redwood forest, 1980, *Norris 55640* (UC); HCRSP, on sawn end grain of fallen log in redwood forest near Rincon Gorge, 1997, 35 m, *KMK 367* (CAS); BBRSP, on bark of redwood tree near Blooms Creek, 2000, 305 m, *KMK 1146* (CAS).

** *Orthotheciella varia* (Hedw.) Ochyra
[*Amblystegium varium* (Hedw.) Lindb.]

Rare; on river bank. Sporophytes unknown from county.

On sandstone rock in San Lorenzo River above Mill Street Dam in Ben Lomond, 90 m, *KMK 1477* (CAS). The site is flooded in summer by the dam, and this rock would often be inundated in winter. Note: Per Crum and Anderson (1981) this habitat is more appropriate for *Hygroamblystegium tenax* (Hedw.) Jenn., but the costa is not broad enough at the base of this specimen, averaging 16–20 μm.

Orthotrichum cupulatum G. F. Hoffmann ex Brid.

Rare; on marble boulders in mixed forest. Sporophytes present on my collection.

FC, "Fall Creek near Felton", year and elevation not listed, *Schofield & Thomas 26441* (UBC, DUKE); FC, forming small clumps on rocks in woods below Blue Cliff, 1999, 285 m, *KMK 657* (CAS).

Note: Vitt (1973) lists *O. cupulatum* from "Fall Creek, near Felton" as Santa Clara Co., but this is in Santa Cruz County. Both collections are from the same location.

* *Orthotrichum diaphanum* Schrad. ex Brid.

Occasional, on the base of trees in city parks. Sporophytes usually present.

On the bark of *Liquidambar* in San Lorenzo Park in Santa Cruz, 2000, 5 m, *KMK 967* (CAS); on wooden roof shingles of small shed in West Lake Park, Santa Cruz, 2001, 75 m, *KMK 1821* (CAS).

Orthotrichum lyellii Hook. & Tayl.

Rare; on tree bark. Sporophytes on the only collection.

On bark of *Quercus wislizenii* on Highway 17 at Laurel Road, 2003, 370 m, *KMK 2712* (CAS). [See note under *O. papillosum*]

* *Orthotrichum obtusifolium* Brid.

Occasional, on coarse bark of *Juglans* and occasionally *Quercus* or *Pseutotsuga*. Sporophytes unknown from county but gemmae common.

On bark of *Salix* near Merk Pond outside of Corralitos, 1999, 60 m, *KMK 720* (CAS); QHR, on bark of *Juglans* near ranch houses, 2000, 170 m, *KMK 947* (CAS); WRSP, on bark of *Pseudotsuga* in sandhill portion of Gray Whale Ranch, 2000, 250 m, *KMK 963* (CAS).

Orthotrichum papillosum Hampe

Abundant on bark of hardwood trees, chaparral shrubs, and occasionally rocks. Sporophytes common.

CRSP, "Castle Rock", 1899, *Dudley s.n.* (CAS); BBRSP, on *Lithocarpus*, 1970, *Franck s.n.* (UC); QHR, on branch of *Quercus* and common throughout park, 1996, 175 m, *KMK 131* (CAS); UCSC, on bark of *Quercus* in second growth redwood forest, 1980, 215 m, *Norris 55677* (UC); HCRSP, on branches of *Acer negundo* along

main entrance road to the park headquarters, 1999, 90 m, *KMK 621* (CAS).

Note: Although this species is not commonly recognized by authors outside of California, there is good reason to do so. Compared to the interior (European) form of *O. lyellii* Hook. & Tayl., there is a distinct difference in leaf shape, and gemmae are never present. Although some overlapping of range occurs, *O. papillosum* is much more common in the coastal areas, and *O. lyellii* is more common inland.

* *Orthotrichum rivulare* Turn.

Common; on seasonally submerged rocks in river and creek beds. Sporophytes always present.

HCRSP, on base of *Alnus* above summer waterline of San Lorenzo River, 1997, 90 m, *KMK 447* (CAS); on sandstone rock in bed of Kings Creek north of Boulder Creek, 2000, 185 m, *KMK 1031* (CAS); on sandstone rock in Majors Creek near the coast, 2000, 25 m, *KMK 1086* (CAS); on granite rock in bed of Carbonera Creek, 2000, 120 m, *KMK 1110* (CAS).

Orthotrichum rupestre Schleich. ex Schwägr.

Occasional; on dry rocks, usually in forest, thus far restricted to the northern half of the county. Sporophytes common.

CRSP, on dry sandstone in shady woods, 1957, *Flowers 5393* (UBC); CRSP, shelf of outcrop in chaparral slope, 1986, *Schofield 87756* (UBC); BBRSP, on sandstone rock in chaparral along China Grade, 2001, 715 m, *KMK 1359*(CAS).

* *Orthotrichum tenellum* Bruch ex Brid.

Common; on trunks of hardwood trees, rarely on rock. Sporophytes almost always present.

QHR, on trunk of *Quercus,* 1996, 215 m, *KMK 304* (CAS); on bark of *Salix* near Merk Pond outside of Corralitos, 1999, 60 m, *KMK 719* (CAS); on bark of apple tree in orchard along Chittendon Road near Aromas, 2000, 30 m, *KMK 929* (CAS); on landscaping rocks around duck pond in San Lorenzo Park in Santa Cruz, 2001, 2 m, *KMK 1832* (CAS).

* *Orthotrichum underwoodii* F. Lara, Garilletti, & Mazimpaka

Rare; on the bark of trees. Sporophytes present on this collection.

On the bark of *Acer negundo* in Felton, 2000, 90m, *KMK 1183* (CAS).

Note: In the short ecology paragraph of the Bryologist article (Garilleti et al. 2001) that describes this species, the two collections are attributed to Santa Cruz County. This is incorrect. The collections are from Santa Clara County, as is stated in the beginning of the paper.

* *Philonotis capillaris* Lindb.

Occasional; on wet or seasonally wet sandstone or soil. Sporophytes unknown from county.

QHR, on vertical wall of small drainage gully through sandstone in chaparral, 2000, 185 m, *KMK 894* (CAS); BBRSP, on thin soil over sandstone outcrop at edge of drainage ditch along China Grade, 2001, 700 m, *KMK 1318* (CAS).

* *Philonotis fontana* (Hedw.) Brid.

Rare; on soil over rock in wet meadows around Boulder Creek. Sporophytes on one of three collections.

BBRSP, on sandstone in Slippery Rock Meadow, 1999, 365 m, *KMK 698* (CAS); among grasses in wet meadow near Boulder Creek Golf Course off Highway 236, 2000, 260 m, *KMK 928* (CAS).

** *Plagiomnium* cf. *cuspidatum* (Hedw.) T. Kop.

Rare; on shaded, wet soil. Sporophytes unknown from county.

On wet soil along a wooden flume above Laguna Creek ca. 1 mile from Highway 1, 2001, 60 m, *KMK 1843* (CAS).

Note: This is a very poor specimen. There is no doubt that this collection is a *Plagiomnium* with teeth only in the distal half of the leaf. It is so small, however, that it is impossible to be confident of the species.

* *Plagiomnium insigne* (Mitt.) T. Kop.

Rare; on leaf litter in redwood forest. Sporophytes unknown from county.

HCRSP, on moist soil in coast redwood forest near creek off the Ox Trail before the railroad tracks, 1998, 85 m, *KMK 586* (CAS).

* *Plagiomnium venustum* (Mitt.) T. Kop.

Rare; on shaded rocks in forest. Sporophytes common.

FC, on marble boulders below Blue Cliff near south fork Fall Creek, 1997, 250 m, *KMK 260 & 557* (CAS).

Plagiothecium laetum B.S.G.

Common; on soil, stumps or logs in forest. Sporophytes common.

On log in redwood forest north of Boulder Creek, 1980, *Norris #55628* (UC); BBRSP, on a redwood stump, 1997, 35 m, *KMK 370* (CAS); WRSP, trailside bank in mixed forest, 1999, 150 m, *KMK 836* (CAS).

* *Platydictya jungermannioides* (Brid.) Crum

Common; on moist soil, rotting wood, stream banks or irrigated gardens and lawns. Sporophytes common.

WRSP, on damp, shaded soil bank of small reservoir in meadow, 1999, 80 m, *KMK 817* (CAS); on dripping wooden posts supporting railroad tunnel in Santa Cruz, 2000, 15 m, *KMK 1093* (CAS); on moist soil at edge of catch basin pond at the base of Loch Lomond dam, 2001, 120 m, *KMK 1535* (CAS); on wet bark of *Salix* branch in the water of Neary's Lagoon in Santa Cruz, 2001, 1 m, *KMK 1828* (CAS).

* *Platyhypnidium riparioides* (Hedw.) Dixon [*Eurhynchium riparioides* (Hedw.) P. Rich]

Rare; found only on submerged rocks in creeks draining the southern flank of Ben Lomond Mountain. Sporophytes unknown from county.

FC, on granite rocks in bed of Barrel Mill Creek, 1999, 305 m, *KMK 679* (CAS); on rocks, submerged and splashed by small waterfall in Laguna Creek, *2001*, 70 m, *KMK 1860* (CAS); submerged to emergent on sandstone rocks in Big Creek in Swanton, 2001, 150 m, *KMK 1901*, (CAS).

Pleuridium acuminatum Lindb.

Difficult to determine abundance due to similarity to *P. subulatum,* on soil in meadows in springtime. Sporophytes usually present.

On poor soil in chaparral, 1996, 235 m, *KMK 190* (CAS); BBRSP, cited in Yip (2001), *Schofield 6452* (NY); sandy soil in chaparral near Ben Lomond, cited in Yip (2001), 1951, *Hesse 695* (UBC).

Pleuridium subulatum (Hedw.) Rabenh.

Difficult to determine abundance due to similarity to *P. acuminatum,* but the two species as an aggregate are very common; on soil in meadows in springtime. Sporophytes usually present.

On shallow soil over bedrock north of Boulder Creek, 1954, 240 m, *Thomas 3715* (CAS); HCRSP, on soil in

grassland, 1999, 180 m, *KMK 594* (CAS); on dry roadside hummocks north of Boulder Creek, cited in Yip 2001, 1962, *Schofield 16774* (UBC); north of Boulder Creek, cited in Yip 2001, 1961, *Hesse s.n.* (UBC).

Pohlia longibracteata Broth. in Röll

Common; on rock or soil on the banks of waterways or seeping walls. Sporophytes occasional.

FNMSP, on sandstone boulders in Aptos Creek near Porter Family Picnic Area, 1994, *Taylor 14661* (UC); HCRSP, on rocks in unnamed creek opposite Ox Trail parking lot on Highway 9 in redwood forest, 1998, 120 m, *KMK 574* (CAS); FC, on wet sandstone bank above north fork Fall Creek, 1999, 240 m, *KMK 680* (CAS); on soil bank above Wilder Creek, 1999, 45 m, *KMK 827* (CAS).

Pohlia nutans (Hedw.) Lindb.

Common; on rock or soil in a variety of habitats, often road cuts. Sporophytes common.

RDO, on vertical road bank in redwood forest along Waddell Creek, 1961, 30 m, *Thomas 9236* (CAS); QHR, on dryer portion of seeping sandstone wall in full sun, 1996, 240 m, *KMK 156* (CAS); HCRSP, on sandy soil in chaparral near campground post 72, 1999, 185 m, *KMK 859* (CAS).

Pohlia pacifica Shaw

Occasional; On moist soil or rock near water. Sporophytes unknown from county.

On sandstone bank of San Lorenzo River in Ben Lomond, 2000, 90 m, *KMK 1164* (CAS); On moist soil near Big Creek in Swanton, 2001, 160 m, *KMK 1906* (CAS); BBRSP, on moist sandstone outcrop near West Berry Creek, 2002, 130 m, *KMK 2495a* (CAS).

Pohlia wahlenbergii (Web. & Mohr.) Andr.

Common; on wet rocks or soil, often around creeks in shade or diffuse light. Sporophytes rare.

Brookdale, Santa Cruz Mountains, 1933, *Morse s.n.* (UC); FC, on a seeping sandstone wall above North Fork Fall Creek, 1999, 245 m, *KMK 705* (CAS); HCRSP, on wet soil of drainage ditch along railroad tracks, 1999, 90 m, *KMK 797* (CAS); LL, on moist shaded mudstone below dam where Newell Creek resumes below Loch, 2001, 120 m, *KMK 1516* (CAS); on shaded sandstone at edge of Laguna Creek upstream of Smith Grade, 2001, 30 m, *KMK 1850* (CAS).

* *Polytrichastrum alpinum* (Hedw.) Sm.

Rare; Soil over rock near water. Sporophytes present on this collection.

BBRSP, soil over rock at edge of Cascade Falls on W. Berry Creek in Redwood Forest, 2002, 215 m, *KMK 2487* (CAS).

Polytrichum juniperinum Hedw.

Common; on poor soils in chaparral, meadows or forest. Sporophytes common in some years.

BBRSP, soil bank of road cut in chaparral, 1999, 610 m, *KMK 736* (CAS); QHR, sandy soil of chaparral-mixed evergreen forest margin, 1996, 175 m, *KMK 124* (CAS); HCRSP, on sandy soil in chaparral, 1999, 195 m, *KMK 644* (CAS); roadside grassy area north of Boulder Creek, 1953, 260 m, *Thomas 2989* (CAS).

* *Polytrichum piliferum* Hedw.

Occasional; on poor soils in chaparral. Often found on sands of inland marine sand deposits. Sporophytes unknown from county.

QHR, sandy soil in chaparral, 1996, 210 m, *KMK 264*

(CAS); HCRSP, sandy soil in chaparral, 1999, 200 m, *KMK 632* (CAS); BDEP, common on sand and sandstone in chaparral, 1999, 610 m, *KMK 740* (CAS).

Porothamnium bigelovii (Sull.) Fleischer in Broth. [*Porotrichum bigelovii* (Sull.) Kindb.]
    Abundant; on soil and rock near waterways, usually above the normal waterline. Occasional on tree bases and soil banks away from water. Sporophytes rare.
    FNMSP, moist soil along Aptos Creek, 1970, *Norris 55631* (UC); BBRSP, "in creek wash on rocks", 1970, *Franck s.n.* (UC); FNMSP, soil bank near stream in redwood forest, 1992, 90 m, *Whittemore 4037* (CAS); HCRSP, on creek bank near San Lorenzo River, 1996, 80 m, *KMK 217* (CAS); WRSP, banks above Wilder Creek, 1999, 45 m, *KMK 860* (UC).

Pseudobraunia californica (Lesq.) Broth.
    Occasional; on dry rocks. Sporophytes common.
    On sandstone wall in meadow north of Boulder Creek, 1997, 200 m, *KMK 332* (UC); on dry roadside rock along Summit Road near CRSP, 1999, 870 m, *KMK 748* (CAS); on north facing sandstone outcrop near Eagle Rock, 2000, 730 m, *KMK 883* (CAS).

Pseudocrossidium obtusulum (Lindb.) Crum & Anderson
    Occasional; on disturbed or poor soils or thin soil over sandstone. Sporophytes not known from county.
    UCSC, on soil among grasses and marble rocks in abandoned quarry, 2002, 135 m, *KMK 2141* (CAS); on moist disturbed soil around San Lorenzo Valley High School near Felton, 2000, 190 m, *KMK 1210a* (CAS). on thin soil over sandstone in grassland above Scotts Valley High School, 2001, 245 m, *KMK 1345* (CAS).

* *Pseudotaxiphyllum elegans* (Brid.) Iwats.
    Occasional; on moist soil banks in coast redwood forest. Sporophytes not known from county.
    BBRSP, on moist soil bank along Skyline to Sea Trail near Kelly Creek, 2002, 180 m, *KMK 2484* (CAS); BBRSP, on dry soil over rock along West Berry Creek, 2002, 235 m, *KMK 2493* (CAS); UCSC, on bank of Cave Gulch Creek, 2003, 200 m, *KMK 2689* (CAS).

Pterogonium gracile (Hedw.) Sm.
    Common; on the bark of hardwood trees or on dry rock. Sporophytes occasional.
    FNMSP, on bark of *Acer macrophyllum* in redwood forest near Aptos Creek, 1980, *Norris 55626* (UC); QHR, on base of *Quercus agrifolia,* 1996, 255 m, *KMK 241* (CAS); BBRSP, on sandstone boulder shaded by *Quercus* along China Grade, 1999, 685 m, *KMK 722* (CAS).
    Note: *KMK 2564* (CAS) is a very odd growth form completely comprised of flagelliform branches. Dried plants exhibit none of the usual "curled bird foot" pattern. It was collected on vertical sandstone rock in Castle Rock State Park.

** *Racomitrium aciculare* (Hedw.) Brid.
    Rare; found only on seasonally flooded rocks in the San Lorenzo River. Sporophytes on 1 of the 2 collections.
    HCRSP, on rocks ca 2 m above waterline in San Lorenzo River (inundated in winter) just downstream from Eagle Creek, 1998, 70 m, *KMK 575* (CAS); HCRSP, on granite boulders in winter river bed of San Lorenzo River just downstream from "Garden of Eden", 1998, 30 m, *KMK 584a* (CAS).

* *Racomitrium elongatum* Ehrh. ex Frisvoll
    Occasional; on sandstone rock outcrops in meadows around Boulder Creek, or on sand in chaparral. Sporophytes unknown from county.

BDEP, on sand along trail in chaparral, 1999, 525 m, *KMK 741* (CAS); BBRSP, on sandstone outcrop in Slippery Rock Meadow, 1999, 365 m, *KMK 696* (CAS).

* *Racomitrium heterostichum* (Hedw.) Brid.
    Occasional on dry rocks in chaparral. Sporophytes uncommon.
    BDEP, on sandstone knob in chaparral, 1996, 520 m, *KMK 139* (CAS); BBRSP, on soil over mudstone in chaparral near Chalk Mountain, 2000, 400 m, *KMK 1078* (CAS).

** *Racomitrium microcarpum* (Hedw.) Brid.
    Rare; on dry sandstone rock outcrop in chaparral. Sporophytes unknown from county.
    On bare sandstone on wall of outcrop in chaparral east of Highway 9 ca ¾ mile north of Boulder Creek, 2000, 230 m, *KMK 1153* (CAS).

* *Racomitrium varium* (Mitt.) Jaeg.
    Occasional; usually on dry rock. 1 collection with sporophytes.
    HCRSP, on granite boulders in flood zone of San Lorenzo River with *R. aciculare,* 1998, 55 m, *KMK 584* (CAS); HCRSP, on bare rock above railroad tracks over concrete trestle, 1999, 90 m, *KMK 651* (CAS); BDEP, on sandstone outcrop in chaparral, 1999, 520 m, *KMK 737* (CAS).

Rhizomnium glabrescens (Kindb.) T. Kop.
    Common; on the shaded banks of creeks or wet logs. Sporophytes rare.
    HCRSP, on rotting logs in Powder Mill Creek near Powder Mill Trail, 1998, 115 m, *KMK 582* (UC); on dripping trailside bank above east branch of Liddell Creek, 1999, 75 m, *KMK 757* (CAS); on sandstone rock in redwood forest at confluence of Waddell and Berry Creeks, 1999, 105 m, *KMK 781* (CAS).

Rosulabryum capillare (Hedw.) Spence
    Very common; On tree trunks, moist soil, concrete, and rotting wood. Sporophytes common.
    On charred redwood stump near Felton, 1949, *Howell #291* (CAS); BBRSP, on fallen burnt tree, 1970, *Franck s.n.* (UC); On burnt log near summit of Hwy 17 in redwood forest, 1954, 550 m, *Thomas 3739* (CAS); FNMSP, moist soil over rotting log at edge of Whites Lagoon, 1999, 430 m, *KMK 778* (CAS); on bark of *Salix* near Soda Lake south of Watsonville, 2000, 45 m, *KMK 913* (CAS); on sandstone bank of San Lorenzo River in Ben Lomond (this site is flooded by a dam for the entire summer, and by high flow for short periods in the winter), 2000, 90 m, *KMK 1171* (CAS).
    Note: I have yet to find any specimen from Santa Cruz County with rhizoidal tubers. As Sayed (1973) uses tuber color to separate similar species such as *B. torquescens,* I have left all collections from this complex in this taxon. See also *Bryum laevifilum.*

Scleropodium californicum (Lesq.) Kindb.
    Occasional; on soil or wood in scrubby areas. Sporophytes unknown from county.
    HCRSP, along San Lorenzo River near entrance bridge, 1979, 75 m, *Whittemore 1117* (CAS); on sandstone rock in brushy area near Majors Creek at Hwy 1, 2000, 30 m, *KMK 1091* (CAS); RDO, at edge of coastal scrub above drainage gully near beach, 2000, 4 m, *KMK 1222* (CAS).

Scleropodium cespitans (C. Müll) L.F. Koch
    Common; on moist rock or rotting wood, or a lawn or garden weed. Sporophytes common.

On charred redwood stump near Felton, 1949, *Howell, 294* (CAS); on bark of *Lithocarpus,* 1970, *Frank s.n.* (UC); HCRSP, on thin soil over rotting wood along Hwy 9, 1999, 100 m, *KMK 604* (CAS); a lawn weed in Harvey West Park in Santa Cruz, 2001, 15 m, *KMK 1238* (UC).

Scleropodium colpophyllum (Sull.) Grout
Common; on moist or dry soil or rotting wood in forests. Sporophytes occasional.
On log in riverine corridor between San Lorenzo River and Hwy 9 in Pogonip Park, 1994, 100 m, *Norris 82246* (UC); QHR, on rotting wood in mixed forest, 1996, 200 m, *KMK 285* (CAS); FC, on dry calcium carbonate formation near Ringtail Creek upstream of Felton-Empire Road, 1999, 425 m, *KMK 597* (CAS).

* *Scleropodium julaceum* Lawt.
Occasional; on dead wood, stone or concrete. Sporophytes occasional.
QHR, on wood and concrete well cover at edge of meadow, 1996, 130 m, *KMK 201* (CAS); on rotting branch of *Alnus* near Majors Creek just upstream of Hwy 1, 2000, 25 m, *KMK 1076* (CAS); on calcareous rock outcrop on Highway 17 at mile marker 8.00, 2003, 350 m, *KMK 2703* (CAS).

Scleropodium obtusifolium (Jaeg.) Kindb. in Mac.
Very common; on seasonally inundated rocks in waterways. Virtually all year round waterways in the county have this plant. Sporophytes rare.
FC, on granitic boulders in Fall Creek, 1961, 200 m, *Thomas 8952* (CAS); on granite rocks in winter flood zone of Carbonera Creek near Scotts Valley, 2000, 120 m, *KMK 1111* (CAS); BBRSP, along seasonal drainage gully in chaparral near SR236, 2001, 550 m, *KMK 1312* (CAS); on sandstone rocks in winter flood zone of Little Creek near Swanton, 2001, 75 m, *KMK 1928* (CAS).

Scleropodium touretii (Brid.) L.F. Koch
Very common; on trailside and roadside banks in forest. Sporophytes occasional.
On redwood stump near Felton, 1946, *Richards et al. 1513* (UC); FNMSP, on soil bank in redwood forest, 1992, 120 m, *Whittemore 4054* (CAS); QHR, on banks of seasonal stream in mixed forest; 1996, 200 m, *KMK 150* (UC); FC, on sandy soil in mixed forest, 1997, 170 m, *KMK 428* (UC).

* *Syntrichia amplexa* (Lesq.) Zander
Rare, on soil. Sporophytes unknown from county.
RDO, at edge of stagnant water in drainage gully at beach, 2000, 1 m, *KMK 1214* (CAS).

** *Syntrichia bartramii* (Steere in Grout) Zand.
Rare; on soil. Sporophytes unknown from county.
On soil at the base of a tree near headwaters of Big Creek near Eagle Rock, 2000, 640 m, *KMK 867* (BUF). Determined by R. Zander.

* *Syntrichia bolanderi* (Lesq. & T. P. James) Zand.
Rare; on moist soil banks. Sporophytes present on one collection.
On soil of roadside bank on Laurel Glen Road north of Soquel, 2002, 125 m, *KMK 2173* (CAS); on soil at the edge of a dirt road near Highway 17 at Laurel Road, 2003, 360 m, *KMK 2650* (CAS).

* *Syntrichia laevipila* var. *laevipila* Brid.
Occasional; on rock and tree trunks. Sporophytes common.
QHR, on *Salix* log in swamp near parking lot, 1996,

160 m, *KMK 130* (CAS); on bark of *Juglans* in meadow south of Eagle Rock, 2001, 650 m, *KMK 1301* (CAS).
Note: These collections differ slightly from European material. The awns have remote teeth and the leaves are unbordered.

** *Syntrichia laevipila* Brid. var. *meridionalis* (Schimp.) Jur.
Occasional; on bark of trees usually but not always with var. *laevipila.* Common on *Juglans hindsii* and *Quercus lobata* in the San Lorenzo Valley. Sporophytes unknown in county.
QHR, on bark of walnut tree (*Juglans*) near ranch houses, 2000, 170 m, *KMK 945* (CAS); on bark of *Quercus lobata* in front of San Lorenzo Valley High School near Felton, 2001, 30 m, *KMK 1205, 1236* (CAS); on bark of *Quercus lobata* in meadow north of Boulder Creek, 2002, 210 m, *KMK 2147* (CAS).
Note: all of these collections have a strong border of thick-walled yellow cells, and the gemmae are costate. This variety is common on trees along Highway 9.

* *Syntrichia latifolia* (Hartm.) Hübener.
Common; on rotting wood or trees near water, but also on thin soil over pavement or a lawn weed. Sporophytes occasional.
WRSP, on bark of *Aesculus californica* near Wilder Creek, 1999, 15 m, *KMK 808* (CAS); HCRSP, on rotting wood in forest near San Lorenzo River, 1999, 75 m, *KMK 842* (CAS); on bark of *Salix* north of Soda Lake near Chittendon, 2000, 45 m, *KMK 921* (CAS); QHR, on thin soil over concrete near ranch houses, 2000, 150 m, *KMK 1192* (CAS).

* *Syntrichia pagorum* (Milde) Amann
Occasional; on the trunks of trees with rough bark. Sporophytes unknown from county.
HCRSP, on bark of *Acer negundo* near beginning of Zayante Trail, 1999, 75 m, *KMK 641* (CAS); on bark of redwood tree in Grant Street Park Santa Cruz, 2000, 4 m, *KMK 1027* (CAS); on bark of *Juglans hindsii* in Ben Lomond, 2001, 100 m, *KMK 1323* (CAS); on bark of *Umbellularia californica* near Rodeo Gulch Rd 0.5 mile north of Soquel Drive, 2001, 45 m, *KMK 2068* (CAS).

* *Syntrichia papillosa* (Wils.) Jur.
Common; on the trunks of trees, often *Juglans,* or in parks, occasionally on concrete. Sporophytes unknown in county.
QHR, on trunk of *Juglans* near ranch houses, 2000, 170 m, *KMK 946* (CAS); on trunk of *Juglans* in meadow near Eagle Rock, 2000, 535 m, *KMK 869* (CAS), on bark of *Liquidambar styracifolia* in San Lorenzo Park, Santa Cruz, 2001, 2 m, *KMK 1840* (CAS).

Syntrichia princeps (De Not.) Mitt.
Common; on rocks and tree trunks. The most common *Syntrichia* species in the county. Sporophytes common.
CRSP, on sandstone Castle Rock, 1957, 915 m, *Heere s.n.* (CAS); QHR, on sandstone rock in oak forest, 1996, 175 m, *KMK 172* (CAS); BBRSP, on sandstone rock in chaparral near Hwy 236, 1999, 500 m, *KMK 703* (CAS); on bark of *Populus trichocarpa* near the Pajaro River east of Watsonville, 2000, 20 m, *KMK 911* (CAS).

Timmiella crassinervis (Hampe) L. Koch
Very common; on soil in diffuse light. Sporophytes occasional.
FC, on ground in redwood forest, 1961, 185 m, *Thomas 8968* (CAS); CRSP, roadside bank in oak woodland, 1986, *Schofield 87753* (UBC); FNMSP, moist soil of road bank

in redwood forest, 1980, *Norris 55619* (UC); QHR, on moist sandy loam under oaks, 1996, 150 m, *KMK 212* (CAS).

Note: There are reports of *T. anomala* from the central coast of California. I have been unable to find any plants that are clearly monoicous.

* *Tortula acaulon* (With.) Zander
[*Phascum cuspidatum* Hedw.]

Occasional; on bare soil patches in pastures. Sporophytes always present.

Among weeds in cow pasture near Eagle Rock, 2001, 660 m, *KMK 1259* (CAS); on bare soil in horse pasture near Felton, 2001, 90 m, *KMK 1283* (CAS); on bare soil in grassland near Hwy. 152, 2002, 160 m, *KMK 2159* (CAS).

* *Tortula atrovirens* (Sm.) Lindb.

Occasional; on sandstone outcrops, on soil in meadows or open chaparral. Sporophytes on all collections.

On exposed sandstone bedrock in grassland north of Scotts Valley, 2001, 245 m, *KMK 1328* (CAS); On sandstone bank in open chaparral along Rodeo Gulch Road mile marker 0.56, 2001, 265 m, *KMK 2062* (CAS); On thin soil over mudstone in coastal pasture north of Davenport, 2002, 75 m, *KMK 2101* (CAS).

* *Tortula muralis* Hedw.

Common; on concrete or mortar, or on rock in chaparral. Sporophytes very common.

QHR, on brick patio near main ranch house, 1996, 155 m, *KMK 146* (CAS); BBRSP, in cracks of sandstone rock in chaparral near Highway 236, 1999, 550 m, *KMK 702* (CAS); on sheltered brick walls near the base of Capitola Wharf on Monterey Bay, 2000, 7 m, *KMK 1196* (CAS); UCSC, on marble foundation of old farm building foundation in sun, 2002, 105 m, *KMK 2132* (CAS).

Note: A few collections of *T. muralis* (*KMK 2132* for example) have mostly muticous leaves with only a few lower leaves with awns. These are reminiscent of *T. plinthobius,* but the peristome is perfect for *T. muralis,* and Flowers (1973) and Crum and Anderson (1981) both describe *T. plinthobius* with at least upper leaves awned.

* *Tortula obtusifolia* (Schwägr.) Mathieu

Common; on disturbed soil. Sporophytes unknown from county.

FNMSP, on disturbed moist calcareous clay, 1999, 115 m, *KMK 686* (CAS); on disturbed soil of road bank near Watsonville, 2000, 15 m, *KMK 932* (CAS); On irrigated soil of planter bed in Capitola, 2000, 30 m, *KMK 1050* (CAS).

* *Tortula subulata* Hedw.

Rare; thus far found only among other mosses on a sandstone outcrop in chaparral. Sporophytes unknown form county.

On protected sandstone outcrop in chaparral near Eagle Rock, 2000, 730 m, *KMK 886* (CAS).

Weissia controversa Hedw.

Common; On soil or rock in diffuse light. Sporophytes common.

QHR, on mudstone rock of *Quercus* forest floor, 1996, 240 m, *KMK 171* (CAS); WRSP, on dry trailside bank protected by roots, 1999, 30 m, *KMK 812* (CAS); RDO, on soil bank in *Quercus-Pinus* forest, 2002, 65 m, *KMK 2085* (CAS).

Zygodon rupestris Schimp. ex Lorentz

Occasional; On the bark of hardwood trees. Sporophytes unknown from county.

HCRSP, On the bark of *Acer* hanging over the San Lorenzo River near Rincon Road, 1999, 30 m, *KMK 669* (CAS); On the bark of *Quercus* in mixed evergreen forest in diffuse light, 2001, 300 m, *KMK 1255* (CAS); QHR, on bark of Quercus, 2001, 160 m, *KMK 1333* (CAS); on bark of *Torreya californica* in the vicinity of Laguna Creek, 2001, 100 m, *KMK 1863* (CAS).

Note: *Zygodon viridissimus* (Dicks.) Brid. reported by Crum (1957), and by Thompson & Ketledge (1958) are probably *Z. rupestris.*

APPENDIX II

UNDESCRIBED SPECIES

Spence has determined that the following two mosses are undescribed. They are both short plants with leaves densely arranged into tight heads in both the wet or dry condition. "A" sometimes has reddish, microphyllous innovations reminiscent of *Pseudotaxiphyllum elegans* in the axils of its leaves. "A" has very short capsules reminiscent of the *B. bicolor* group, while "B" has much longer, more cylindrical capsules.

Bryum sp. A

Rare; on dry sandstone formations. Sporophytes present on this collection.

On vertical sandstone wall in grassland above the Scotts Valley High School, 2001, 250 m, *KMK 1350* (CAS).

Bryum sp. B

Common; on dry sandstone formations, particularly around QHR.

QHR, on vertical face of sandstone rock outcrop in Ponderosa Pine Parkland, 2000, 175 m, *KMK 1139* (CAS); BBRSP, on sandstone outcrop in chaparral off Highway 236 near China Grade, 2001, 575 m, *KMK 1315* (CAS); on sandstone rock outcrop in meadow 1 km north of Boulder Creek on Highway 9, 1958, 175 m, *J.H. Thomas 6999* (CAS).

Orthotrichum sp. A

This specimen has been determined by Dan Norris to be new to science. Both Dale Vitt and Bernard Goffinet concur (personal communication). It is known only from one small boulder field in Santa Cruz County, and a second very small population in southern San Mateo County. The moss is characterized by creeping stems and a differentiation between the leaves on the vegetative and perichaetial axes.

Rare; on dry rock in chaparral. Sporophytes on this one collection.

BBRSP, on boulders eroded out of base sandstone in chaparral, 2001, 685 m, *KMK 1251* (CAS).

* *Schistidium* sp. A

Determined by Blom to represent an as yet undescribed species related to *S. cinclidodontium* (C. Müll.) Brem. The leaf lacks the long-channeled apex that is present on *S. cinclidodontium.*

Rare, known only from dry sandstone rock. Sporophytes present on this one collection.

On dry sandstone and soil over sandstone near Eagle Rock, 2001, 750 m, *KMK 1340* (CAS & Blom pers. herb.).

* *Schistidium* sp. B

Determined by Blom to represent an as yet undescribed segregate species in the *S. apocarpum* group, related to *S. pulchrum* Blom. The plant is larger in all respects than

that species, with a longer, narrowly oblong-cylindrical capsule.

Rare, known only from dry sandstone rock. Sporophytes present on this one collection.

BBRSP, on sandstone rock in opening in mixed forest near China Grade, 2001, 680 m, *KMK 1356* (CAS & Blom pers. herb.).

* *Tortula* sp. A

Dan Norris has determined these collections to represent an as yet undescribed species. These are small plants, related to *Tortula guepinii* (Bruch & Shimp. in B.S.G.) Zand. with very short leaves with a flexuose hyaline awn and a very large costal pad comprised of cells that are taller than wide (reminiscent of *Tortula atrovirens*). The upper cells are densely papillose with branched papillae. The margins are recurved and have a narrow border with less papillose cells.

Rare; on rock in chaparral or coastal scrub. Sporophytes common.

On mudstone rock in coastal scrub above Liddell Creek near Davenport, 2001, 65 m, *KMK 1533* (pers. herb.).

Taxiphyllum sp. A

Determined by Ireland to probably be a new species in the genus *Taxiphyllum* (Mitt.) Fl. It is characterized by very small cultriform leaves with serrulate margins and foliose pseudoparaphyllia.

The plants are strongly complanate.

Rare; on limestone or marble rock in coast redwood forest. Sporophytes unknown.

FC, on marble near the lime kilns, 1999, 200 m, *KMK 704* (Ireland pers. herb.); UCSC, on limestone rock in Cave Gulch, 2003, 195 m. *KMK 2671.* (Ireland pers. herb.)

APPENDIX III

POSSIBLE ADDITIONS TO THE FLORA

Aloina bifrons (DeNot.) Delgadillo. Mapped in the Bay Area by Delgadillo (1975).

Antitrichia curtipendula (Timm ex Hedw.) Brid. Four collections in San Mateo Co. (CAS, UC), also cited in Thompson and Ketledge (1958) in Santa Clara Co.

Barbula eustegia Card. & Ther. A collection in NY was listed in the database, but I have not examined it.

Bryum gemmascens Kindb. Cited in Sayed (1973) from Santa Clara County.

Campylopus introflexus (Hedw.) Brid. Known from Marin and Monterey Counties (UC) and from San Francisco and San Mateo Counties (CAS).

Claopodium crispifolium (Hook.) Ren. & Card. Has been reported from Marin Co. by Yurky (1990), and there is a collection from San Mateo Co. in UC.

Homalothecium nevadense (Lesq.) Ren. & Card. Collections from Alameda Co. and Monterey Co., both in UC.

Orthodontium pellucens (Hook.) Bruch & Schimp. in B.S.G. known from redwoods in Monterey Co. (UC).

Orthotrichum bolanderi Sull. Collection from Monterey Co. (UC) and Santa Clara Co. (CAS, MO). Also cited in Steere et al. (1954), and Vitt (1973).

Orthotrichum consimile Mitt. Collection in UC from Marin Co., and one from San Francisco Co. in CAS.

Philonotis americana (Dism.) Dism. Reported by Zales (1973) for Santa Cruz County. I have not seen the specimen.

Physcomitrium pyriforme (Hedw.) Hampe Collection in CAS from San Mateo Co.

Timmiella anomala (Bruch. in Schimp. in B.S.G.) Limpr. Collection in CAS from San Francisco, and one in UC from Monterey Co.

Tortula brevipes (Lesq.) Broth. Whittemore collections in CAS from Santa Clara Co.

Triquetrella californica (Lesq.) Grout Collections from San Francisco Co. (CAS) and Contra Costa Co. (NY).

APPENDIX IV

MOSSES BY HABITAT

Lawn Weeds

Amblystegium juratzkanum, Amblystegium serpens, Barbula unguiculata, Brachythecium albicans, Brachythecium rutabulum, Eurhynchium praelongum, Leptodictyon riparium, Platydictya jungermannioides, Scleropodium cespitans, Syntrichia latifolia.

Grasslands

Acaulon muticum, Aloina aloides, Archidium alternifolium, Barbula unguiculata, Bartramia stricta, Bruchia flexuosa, Bryum argenteum, Bryum capillare, Bryum bicolor, Bryum gemmilucens, Ceratodon purpureus, Didymodon vinealis, Ditrichum shimperi, Entosthodon attenuatus, Ephemerum serratum, Fissidens curvatus, Fissidens crispus, Fissidens sublimbatus, Funaria hygrometrica, Hennediella heimii, Hennediella stanfordensis, Homalothecium arenarium, Microbryum davallianum, Microbryum starkeanum, Pleuridium acuminatum, Pleuridium subulatum, Polytrichum juniperinum, Timmiella crassinervis, Tortula acaulon.

Tree Bark

Alsia californica, Antitrichia californica, Bryolawtonia vancouveriensis, Bryum capillare, Bryum laevifilum, Dendroalsia abietina, Dicranoweisia cirrata, Dicranum fusescens, Dicranum tauricum, Didymodon nicholsonii, Eurhynchium praelongum, Fabronia pusilla, Homalothecium nuttallii, Hypnum circinale, Isothecium cristatum, Isothecium myosuroides, Isothecium obtusatulum, Neckera douglasii, Orthotrichum diaphanum, Orthotrichum lyellii, Orthotrichum obtusifolium, Orthotrichum papillosum, Orthotrichum tenellum, Orthotrichum underwoodii, Pterogonium gracile, Syntrichia laevipila, Syntrichia laevipila var. *meridionalis, Syntrichia latifolia, Syntrichia pagorum, Syntrichia papillosa, Syntrichia princeps, Zygodon rupestris.*

Leaf Litter

Bryum canariense, Eurhynchium oreganum, Scleropodium californicum, Plagiomnium insigne.

Rotting Wood

Bryum capillare, Dicranoweisia cirrata, Dicranum tauricum, Eurhynchium praelongum, Isothecium cristatum, Isothecium myosuroides, Orthodontium gracile, Syntrichia latifolia.

Aquatic

Brachythecium starkei, Crumia latifolia, Dichodontium pellucidum, Eurhynchium hians, Fissidens bryoides, Fissidens crispus, Fissidens grandifrons, Fissidens ventricosus, Hygrohypnum bestii, Leptodictyon riparium, Platyhypnidium riparioides.

Creek Banks and Stranded Rocks in Creek Beds

Bestia longipes, Blindia acuta, Brachythecium asperrimum, Brachythecium frigidum, Bryolawtonia vancouveriensis, Bryum gemmiparum, Calliergonella cuspidata, Dichodontium pellucidum, Didymodon insulanus, Didymodon rigidulus, Eurhynchium praelongum, Fissidens bryoides, Fissidens taylorii, Grimmia lisae, Leucolepis acanthoneura, Metaneckera menziesii, Mnium marginatum, Orthotheciella varia, Orthotrichum rivulare, Pohlia longibracteata, Pohlia pacifica, Pohlia wahlenbergii, Polytrichastrum alpinum, Porothamnium bigelovii, Pseudotaxiphyllum elegans, Racomitrium aciculare, Racomitrium varium, Rhizomnium glabrescens, Scleropodium obtusifolium.

Disturbed Places and Very Poor Soils

Acaulon muticum, Aloina aloides, Barbula unguiculata, Bryum barnesii, Bryum bicolor, Bryum canariense, Bryum capillare, Bryum gemmilucens, Bryum violaceum, Bryum subapiculatum, Bryum sp. B, Chenia leptophylla, Ceratodon purpureus, Ceratodon stenocarpus, Didymodon brachypyllus, Didymodon insulanus, Didymodon vinealis, Fissidens curvatus, Funaria hygrometrica, Funaria muhlenbergii, Hennediella heimii, Hennediella stanfordensis, Homalothecium arenarium, Pleuridium acuminatum, Pleuridium subulatum, Pohlia nutans, Polytrichum juniperinum, Polytrichum piliferum, Pseudocrossidium obtusalum, Timmiella crassinervis, Tortula acaulon.

Dry Rocks

Aloina rigida, Bryum sp. A, Bryum sp. B, Crossidium aberrans, Crossidium squamiferum, Didymodon brachyphyllus, Didymodon insulanus, Didymodon nicholsoni, Didymodon norrisi, Didymodon rigidulus, Didymodon vinealis, Fissidens sublimbatus, Grimmia laevigata, Grimmia lisae, Grimmia montana, Grimmia ovalis, Grimmia trichophylla, Grimmia ungeri, Gymnostomum aeruginosum, Hedwigia stellata, Homalothecium nuttallii, Homalothecium pinnatifidum, Orthotrichum cupulatum, Orthotrichum papillosum, Orthotrichum rupestre, Orthotrichum sp. A, Pseudobraunia californica, Racomitrium elongatum, Racomitrium heterostichum, Racomitrium microcar-
pum, Racomitrium varium, Schistidium sp. A, Schistidium sp. B, Syntrichia princeps, Tortula muralis, Tortula sp. A.

Concrete and Pavement

Bryum argenteum, Bryum capillare, Ceratodon purpureus, Didymodon insulanus, Funaria hygrometrica, Grimmia pulvinata, Homalothecium nuttallii, Syntrichia latifolia, Syntrichia princeps, Tortula muralis.

Irrigated Gardens

Amblystegium serpens, Barbula unguiculata, Brachythecium albicans, Bryum gemmiferum, Didymodon tophaceus, Drepanocladus aduncus, Hennediella stanfordensis, Platydictya jungermannioides, Tortula obtusifolia.

Soil Banks

Atrichum selwynii, Atrichum undulatum, Claopodium whippleanum, Ditrichum ambiguum, Epipterygium tozeri, Eurhynchium praelonga, Fissidens crispus, Fissidens pauperculus, Isothecium cristatum, Isothecium myosuroides, Porothamnium bigelovii, Pseudotaxiphyllum elegans, Scleropodium touretii, Syntrichia bolanderi, Timmiella crassinervis.

Immediate Coast

Amblystegium juratzkanum, Bryum argenteum, Bryum barnesii, Bryum gemmilucens, Bryum gemmiparum, Didymodon vinealis, Didymodon rigidulus, Eurhynchium praelongum, Fissidens crispus, Funaria hygrometrica, Hennediella heimii, Homalothecium arenarium, Mielichhoferia elongata, Scleropodium californicum, Tortula muralis.

Winter Ephemerals

Although some of these plants are not annuals, they are included here because they are almost never found outside of the winter or spring.

Acaulon muticum, Bruchia flexuosa, Entosthodon attenuatus, Ephemerum serratum, Hennediella heimii, Hennediella stanfordensis, Microbryum davallianum, Microbryum starkeanum, Pleuridium acuminatum, Pleuridium subulatum, Tortula acaulon, Tortula obtusifolia.

GERMINATION, EARLY GROWTH, AND FLOWERING OF A VERNAL POOL ANNUAL IN RESPONSE TO SOIL MOISTURE AND SALINITY

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Abstract

Vernal pools are temporary wetlands typical of regions with mediterranean climates. Within a region, variation in substrate and topography of vernal pools may expose plants to varied soil moisture and salinity conditions. We examined the effects of soil moisture and salinity on germination, growth, flowering, and mortality of a California endemic vernal pool annual, *Lasthenia conjugens* E. Greene (Asteraceae). We collected seeds from three source populations and subjected them to two moisture treatments and three salinity treatments under greenhouse conditions. We detected significant differences in germination, growth, floral initiation, and mortality among source populations, moisture treatments, and salinity treatments. We also found evidence of significant population by treatment interactions for germination and floral initiation in the salinity experiment, suggesting that source population affects viability under varying salinities. Increased salinity generally had detrimental effects on germination and growth rates of seedlings, but populations varied in their responses to the salinity treatments. We conclude that 1) because source populations varied in their response to soil moisture and salinity, seed source for population reintroduction should be carefully selected, and 2) moisture and salinity treatments produced strong effects on *L. conjugens* seeds and seedlings. Thus, year-to-year variation in rainfall, soil salinity, and inundation of individual pools may significantly affect the performance of *L. conjugens* individuals and populations.

Key Words: Annual plants, California grasslands, *Lasthenia conjugens,* restoration, wetlands.

Vernal pools are spatially discrete, ephemeral wetlands typical in regions with mediterranean climates (Zedler 1987; Dallman 1998; Keeley and Zedler 1998). Distinct wet and dry seasons lead to winter and spring inundation of pools, followed by complete drying in summer. These temporary wetlands, characteristically underlain by an impervious hardpan (Holland and Jain 1977), support a unique biota capable of withstanding and responding to extreme variation in physical conditions (Stebbins 1976; Zedler 1987; Keeley and Zedler 1998). For example, California's vernal pools harbor more than 60 known endemic species of plants and invertebrates (Holland 1978; Stone 1990; Baskin 1994).

Vernal pools are also unpredictable environments. Annual variation in timing and amount of rainfall in California results in large year-to-year differences in vernal pool hydrology (Hanes and Stromberg 1998), and therefore in the onset and duration of the growing season (Zedler 1984; Bliss

and Zedler 1998). Annual species are prominent in vernal pool communities (Zedler 1987, 1990) and typically, life cycles of both plants and invertebrates are completed in the variable period of time when soils are moist to inundated. In such an unpredictable environment, germination cues are of central importance to seed-dependent annuals (Keeley 1988; Zammit and Zedler 1990). For example, emergence too late in the wet season may result in reproductive failure, but premature germination could be fatal if seasonal precipitation is insufficient. Ideally, germination would occur as soon as ample precipitation has fallen to promote plant growth and early survival (Bliss and Zedler 1998).

Annual variation in vernal pool hydroperiod has also been linked to strong year-to-year variation in the composition of vernal pool plant communities (Griggs 1980; Holland and Jain 1984; Bliss and Zedler 1998). If species have dissimilar germination cues, then particular precipitation regimes may favor certain species over others. For example, Bliss and Zedler (1998) exposed field-collected vernal pool soils to precipitation regimes that varied in timing of first soil moistening, length of moist

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period before inundation, and length of inundation. Overall, timing of first moistening was the most important factor affecting both number of plants and the number of species that germinated in the study, but individual species varied in response to different treatments. The authors concluded that vernal pool plants are potentially very sensitive to the timing of the initial rains each year. Annual variation in precipitation may thus partially explain variation in plant abundance and species composition among pools or among sites (Holland and Jain 1984; Baskin 1994).

Vernal pools were once widespread along the Pacific coast and Central Valley of California (Barbour et al. 1993; Bauder and McMillan 1998). Urban expansion and agricultural development have destroyed most of the vernal pool habitat in California, and it is estimated that only 3–10 percent of pools remains (Holland and Jain 1977; Baskin 1994; Holland 1998). *Lasthenia conjugens* E. Greene (Contra Costa goldfields: Asteraceae) (Hickman 1993) is a showy spring annual that has declined as a consequence of vernal pool habitat loss in northern California (Ornduff 1966; Sawyer and Keeler-Wolf 1995). Although historically more abundant and widespread, *L. conjugens* is currently known from fewer than 20 populations in four counties (Federal Register 1997). Because of population declines and local extinctions caused by habitat loss, *L. conjugens,* along with a number of other vernal pool endemics, was recently listed as endangered under the federal Endangered Species Act (ESA) (Federal Register 1997). Because of its rarity, conservation of existing populations, as well as restoration and reintroduction of populations will be critical aspects of recovery for this species. The success of these reintroductions will depend, in part, on knowledge of target species' life history and habitat requirements (Pavlik et al. 1993; DeMauro 1994; Helenurm 1998), many details of which are currently scarce.

Detailed studies of spatial and temporal variation in abundance and distribution of *L. conjugens* are lacking. However, our observations and those of others suggest, first, that population size can vary tremendously from year to year (Ornduff 1966; Dains 1995), and at one site for which we have data for several years, appears to be greater in wetter than drier years (Collinge and Marty unpublished data). Second, *L. conjugens* occurs on soils ranging from alkaline/saline to neutral, but populations tend to be larger on neutral sites than alkaline or saline sites (Dains 1995; Vollmar Consulting 1997). Dains (1995, p. 9) observed, ". . . increasing alkalinity/salinity of the soil seems correlated with decreased cover of Contra Costa Goldfields." Small populations at three large alkaline/saline sites (e.g., Potrero Hills landfill, San Francisco National Wildlife Refuge, and Ft. Ord; Collinge personal observation; H. Forbes personal communication) and larger populations at less alkaline/saline sites (e.g., Travis Air Force Base) lead to the suggestion that saline conditions may represent marginal habitat for *L. conjugens.*

Given the potential importance of variable precipitation for vernal pool plant germination, growth, and development, and the potential for *L. conjugens* populations to be limited by soil salinity conditions, we examined the effects of two soil moisture levels and three soil salinity levels on germination, early growth, floral initiation, and mortality of *L. conjugens* collected from three populations in northern California. We predicted first, that *L. conjugens* germination, growth, and development would be positively related to soil moisture. If so, then this response would at least partially explain reported variation in annual population size. Second, because maternal parent can have large fitness-related consequences for offspring (Antonovics and Schmitt 1986; Dudash et al. 1997), we predicted that the maternal family from which seeds came would significantly influence their response to soil moisture. We were unable to examine the influence of maternal parent on response to soil salinity due to insufficient seed availability. Third, we hypothesized that *L. conjugens* germination, growth, and development would be negatively related to soil salinity, given field observations of smaller populations under more saline than less saline conditions. And fourth, we expected that the three source populations would differ in their response to varying soil salinity, given that they naturally occurred on soils that varied in salinity.

MATERIALS AND METHODS

Source Populations

We obtained *L. conjugens* seeds from three populations in northern California (38°30′N, 122°30′W), designated as Napa, Travis, and Potrero. The three populations occur north of San Pablo and Grizzly Bays, which are northern and eastern extensions, respectively, of the San Francisco Bay. The three populations are located within approximately 25 km of each other; yet appear to occur under different soil salinity conditions, given their differential proximity to brackish water. Seeds from Napa were collected and donated for this experiment by the late Dr. Robert Ornduff (University of California, Berkeley) from a population composed of several thousand plants. These seeds were collected in 1994 from a large vernal pool in a sloping pasture at the eastern edge of Highway 121, approximately 1 km west of the Napa River (Ornduff personal communication). Soil salinity and plant community composition at this site were not recorded, but the population occurs at approximately 70 m elevation and 15 km from San Pablo Bay. This site is underlain by basalt (Ornduff personal communication) and it is likely that it was historically more influenced by freshwater than saline conditions. This site has recently been developed into agricul-

tural land and few, if any *L. conjugens* individuals or other native vernal pool species remain (B. Weaver personal observation). The Napa seeds had been in cold storage for several years, and were not separated by maternal parent.

We collected seeds in May 1999 from Travis Air Force Base, Solano County, California, from a 15-ha vernal pool complex near the Aero Club facilities on the northwest corner of the base (Collinge 1999). This seed collection was designed primarily for a large field experiment, and we used extra seeds for this greenhouse study. We collected seeds from 5–20 randomly selected individual plants per pool (n = 80 pools throughout the 15-ha site), and placed seeds from each plant into a separate coin envelope. The Travis population is one of the largest remaining populations of *L. conjugens,* containing tens of thousands of individuals (Collinge and Marty unpublished data). At this site, *L. conjugens* co-occurs with other native vernal pool species, the most common of which are *Downingia concolor* var. *concolor* (Downingia, Campanulaceae), *Layia chrysanthemoides* (tidy tips, Asteraceae), *Plagiobothrys stipitatus* var. *stipitatus* (popcornflower, Boraginaceae), *Deschampsia danthonioides* (annual hairgrass, Poaceae), and *Eryngium vaseyi* (button celery, Apiaceae) (Hickman 1993) (Collinge and Marty unpublished data). Available data from *L. conjugens* populations elsewhere at Travis AFB suggest that soil salinity is relatively low, ranging from approximately 0.22–0.67 mmhos (Dains 1995; Vollmar 1997).

The Potrero population occurs in a wetland area near the Potrero Hills landfill, approximately 5 km south of Travis AFB. This population is relatively small, containing less than two hundred individuals (Dains 1995). The site borders a historic tidal marsh near Grizzly Bay, forming an alkaline seasonal wetland with an adjacent upland (Dains 1995). Plant species composition at the Potrero site is quite different from that at Travis AFB, suggesting more saline conditions. At Potrero, *L. conjugens* co-occurs with the salt- and alkali-tolerant *Cotula coronopifolia* (brass-buttons, Asteraceae), *Distichlis spicata* (saltgrass, Poaceae) and *Salicornia* sp. (pickleweed, Chenopodiaceae) (Hickman 1993) (Dains 1995; Collinge personal observation). In June 1998, we collected seeds from 40 randomly selected individuals from a 4-ha area of the approximately 12-ha Potrero site and placed them in separate coin envelopes.

Greenhouse Experiments

To investigate the influences of soil moisture, soil salinity, and maternal family on germination, growth, flowering, and mortality of *L. conjugens* from the source populations, we conducted two controlled greenhouse experiments at the University of Colorado, Boulder. For the soil moisture experiment, our experimental design was a two-by-

two factorial with two source populations (Napa and Potrero) and two soil moisture treatments (moist, wet). In addition, for the Potrero population, our design included maternal family nested within moisture treatment. For the soil salinity experiment, our factorial experimental design used three source populations (Napa, Travis, and Potrero) and three salinity treatments (low, medium, and high salinity) plus a control treatment (tap water).

In both experiments, we used a sandy loam soil mixture composed of 13.3% clay, 8.5% silt, 51.6% medium-to-very fine sand, and the remainder coarse sand. It contained <2% organic matter and had a neutral pH (T. Lemieux personal communication). We chose this soil because of its similarity to native soils in which *L. conjugens* occurs in the three study populations (Dains 1995; Ornduff personal communication). Soils at Travis are classified as Antioch San Ysidro complex and San Ysidro sandy loam, and at Potrero as Pescadero clay loam (Dains 1995; Vollmar 1997). Collecting a sufficient volume of soil from any of the field sites for these experiments would have been ethically questionable given the dramatic loss of vernal pool habitats in northern California. Throughout both experiments, we controlled greenhouse temperature to approximate winter conditions in the California vernal pool sites where the seeds were collected. Daytime temperatures fluctuated between 15 and 21°C, and nighttime temperatures between 2 and 10°C.

Soil moisture experiment.

We planted 504 seeds from the Napa population and 520 seeds from the Potrero population in square plastic pots (7 × 7 × 7 cm), with four seeds to a pot. Seeds were planted approximately 2–3 mm under the soil surface. Half the seeds from each population were subjected to wet conditions, and half to moist conditions, described in detail below. Because Potrero seeds had been collected by maternal family, each maternal parent was randomly assigned to one of the two moisture treatments and twenty of its seeds were planted (n = 13 maternal parents per moisture treatment).

We subjected seeds from each population to two moisture treatments. The wet treatment consisted of pots placed in plastic, rectangular trays (27.5 cm wide × 53.5 cm long × 6 cm deep) filled with 4 cm of water. For the moist treatment, we placed pots in identical plastic trays and filled the trays with approximately 0.5 cm of water. Water in the moist treatment trays evaporated within 24 hr, but water in the wet treatment trays did not evaporate between watering. For the first 14 d of the experiment, we refilled trays to the specified levels every 24 hr and recorded germination each day. After 14 d, the major flush of germination had occurred, so thereafter we refilled trays and recorded germination every other day until day 60 of the experiment. Wet tray water levels fluctuated between 1.5 and 4

cm of water, and moist trays fluctuated between 0 and 0.5 cm of water. We rotated trays every other day throughout the experiment to control for any systematic environmental variation across greenhouse benches.

To compare soil moisture among treatments, we filled 15, 7 × 7 × 7 cm pots with soil as described above and watered them similarly to the pots containing seeds (n = 7 moist, 8 wet). After 60 d, we determined soil moisture content by drying soil at 105°C, recording the amount of water lost per unit weight of soil, and relating this percentage soil moisture to the water-holding capacity of a sandy loam soil (Kramer 1983).

Soil salinity experiment.

We planted 400 seeds from each of three populations (Napa, Travis, and Potrero; 1200 seeds total) in square plastic pots (9 × 9 × 9 cm), with 4 seeds per pot. Five pots from each population were placed into rectangular trays, with 5 trays per salinity treatment (n = 25 pots/treatment × 4 seeds per pot = 100 seeds per population/treatment combination). The position of the pots within the trays was randomized in order to control for any systematic environmental variation across greenhouse benches. We filled the trays to a depth of 5 cm tap water on the day the seeds were planted. Two days were allowed for the soil to absorb the water and then the salinity treatments were imposed. We prepared three salinity treatments from a synthetic sea salt (Instant Ocean, Aquarium Systems, Inc., Mentor, OH). The salinity treatments were 5 parts per thousand (ppt) of Instant Ocean (10 g salt with 2 liter tap water), 12.5 ppt (25 g salt with 2 liter of tap water), and 20 ppt (40 g salt with 2 liter tap water). We chose these salinity levels to span the expected range of salinity values to which *L. conjugens* plants from these populations are exposed in the field. Saline solutions (salinity treatments) or tap water (control pots) were poured into the trays and absorbed into the soil of each pot. After the salinity treatments were added, the trays were filled to a depth of 5 cm tap water everyday for the remainder of the experiment.

Plant Measurements

We recorded germination and seedling mortality, and monitored early seedling growth for plants in both experiments. In the soil moisture experiment, we measured seedling heights 10 d, 4 wk, and 7 wk after germination. Seedling mortality was recorded every other day for the duration of the experiment. On a per plant basis, we recorded floral initiation when flower buds were observable, and recorded flowering when flowers completely opened. Because *L. conjugens* is self-incompatible (Ornduff 1966), we did not include seed production in our measurements, and we terminated the experiment after 130 d, at which point plants were be-

ginning to senesce. In the soil salinity experiment, both seedling heights and seedling mortality were recorded at 2 wk, 4 wk, and 6 wk after germination. We also recorded which plants initiated flowers and terminated this experiment at 90 d.

Data Analyses

For both experiments, we calculated overall percent germination (number seeds germinated/number seeds planted) and seedling mortality (number seedlings dead/number seeds germinated) in all treatment combinations. We also calculated the percent of individuals that initiated flowers and that flowered as the number of individuals in that category divided by the number of individuals that germinated. To compare plant responses among source populations and moisture or salinity treatments, we used χ^2 tests (Sokal and Rohlf 1995), which tested the null hypotheses that number of seeds germinated, the number of plants that initiated flowering or flowered, and the number of dead seedlings was independent of source population and moisture or salinity treatment.

For all further analyses, we calculated the mean response variable (e.g., days to emergence, height) for the four seedlings per pot because seedlings within pots were considered to be non-independent. Because our experimental design for the moisture experiment included family structure for the Potrero population but not the Napa population, we conducted separate analysis of variance (ANOVA) for each population because the pots containing siblings from the Potrero population could not be treated as independent and equal to pots of unrelated seeds from the Napa population.

Because pots within trays may be non-independent as well, we performed nested analyses to assess the variance among trays. In both experiments, for those seeds that germinated, we calculated the number of days to emergence using a nested ANOVA that included the main effects of treatment and population (salinity experiment only), the nested effect of tray within treatment, and the interaction of treatment and population (salinity experiment only). We also calculated overall percentages of plants that initiated flowers and flowered, and for those that did so (soil moisture experiment only), the number of days to floral initiation and flowering. For the flowering data we could not assess the nested effect of tray within treatment because too few plants initiated flowers across the various treatment combinations.

For the salinity experiment, we used the Tukey-Kramer mean comparison procedure (Sokal and Rohlf 1995) to compare emergence times for seeds from the three populations in the four treatments. We chose this method because it is appropriate for unequal sample sizes among groups, and we had unequal numbers of seeds that germinated among treatments and populations.

Because we recorded seedling heights several times during both experiments, we used a nested, repeated measures ANOVA to assess the main effects of treatment and population (salinity experiment only), the nested effect of tray within treatment, the interaction of treatment and population (salinity experiment only), and changes in these effects over time. This analysis is appropriate when measurements are not independent from one another, such as repeated measurements on a single individual. We performed sphericity tests (SAS Institute 2001) to determine whether to interpret adjusted or unadjusted univariate F-tests.

We used a nested ANOVA to examine effect of maternal plant on seedling growth for the Potrero population in the soil moisture experiment. Twenty-six maternal plants were used for this analysis (n = 13 per moisture treatment). For the maternal plant analysis, we compared seedling heights at 7 weeks among moisture treatments, and among families within treatment.

To compare soil moisture between the wet and moist treatments in the soil moisture experiment, we compared percent soil moisture using a t-test. We transformed the percent soil moisture values using the arcsine-square root (p) transformation, where p = proportion soil moisture (Sokal and Rohlf 1995). We used the statistical package JMP Version 4 for all statistical analyses (SAS Institute 2001).

RESULTS

Soil Moisture Experiment

Our watering regime effectively varied soil moisture level, as expected. Soil moisture differed significantly among treatments (t-test, $t_{1,13}$ = 12.09, P < 0.001). The wet treatment soils contained an average of 27.0 % (SE ± 0.001) water, while the moist treatment contained 24.1% (SE ± 0.001) water. These values conform to field capacity of a sandy loam soil for the wet treatment and slightly less than field capacity for the moist treatment (Kramer 1983).

Lasthenia conjugens seeds germinated readily under greenhouse conditions. Overall germination exceeded 70% for three of the four moisture treat-

ments (Table 1), but depended significantly on source population and moisture treatment. For seeds from the Potrero population, more seeds germinated in the moist treatment than in the wet treatment (Table 1), while for seeds from the Napa population, more seeds germinated in the wet treatment than in the moist treatment. Hence, seeds from the two source populations exhibited opposite germination responses to the moisture treatments.

We observed similar patterns for floral initiation (Table 1), which was significantly affected by source population and moisture treatment. As with germination, more individuals from the Potrero population initiated flowers in the moist treatment than the wet treatment, while for seeds from the Napa population, more individuals initiated flowers in the wet treatment. No individuals from the Potrero population flowered (Table 1), so it was not possible to evaluate the effect of source population for this variable. Twenty-nine individuals from the Napa population flowered, however, with a higher number of individuals flowering in the wet treatment than in the moist treatment. Seedling mortality was not significantly associated with population or moisture treatment, although it exceeded 50% overall (Table 1).

Lasthenia conjugens seeds germinated quickly, beginning four days after planting for both moisture treatments and populations (range = 4–28 d). For those plants that germinated, time to emergence depended significantly on moisture treatment (nested ANOVA treatment effect, Fig. 1, Table 2).

In the Napa population but not the Potrero population, plants in the wet treatment developed flowers more quickly than those in the moist treatment (Fig. 2, Table 2). For both populations, plants in the wet treatment grew faster than plants in the moist treatment throughout the experiment (time*treatment interaction, Fig. 3, Table 3).

Maternal family in the Potrero population significantly affected seedling growth (nested ANOVA family [treatment] effect, $F_{23,1}$ = 2.34, P = 0.0011). Seedling heights among families at 7 wk of age ranged from 27.6 to 50.0 mm for the moist treatment and from 37.0 to 75.5 mm for the wet treatment.

TABLE 1. NUMBER AND PERCENT OF SEEDS GERMINATED, SEEDLING FLORAL INITIATION, FLOWERING, AND MORTALITY IN *L. CONJUGENS* IN THE SOIL MOISTURE EXPERIMENT. Germination percent was calculated as the number germinated divided by the number planted. Floral initiation, flowering, and mortality were calculated as the number of individuals in that category divided by the number of individuals that germinated. [a] $\chi^2_{[1]}$ = 4.29, P<0.05. [b] $\chi^2_{[1]}$ = 12.81, P<0.005. [c] Test could not be performed because of zero values for Potrero population. [d] $\chi^2_{[1]}$ = 0.32, P>0.50.

Population and treatment	Number planted	Germination[a] Number (percent)	Floral initiation[b] Number (percent)	Flowering[c] Number (percent)	Mortality[d] Number (percent)
Potrero moist	260	211 (81.2)	32 (15.2)	0 (0)	130 (61.6)
Potrero wet	260	179 (68.8)	16 (8.9)	0 (0)	104 (58.1)
Napa moist	252	184 (73.0)	48 (26.1)	5 (2.7)	166 (90.2)
Napa wet	252	210 (83.3)	83 (39.5)	24 (11.4)	120 (57.1)

1.

2.
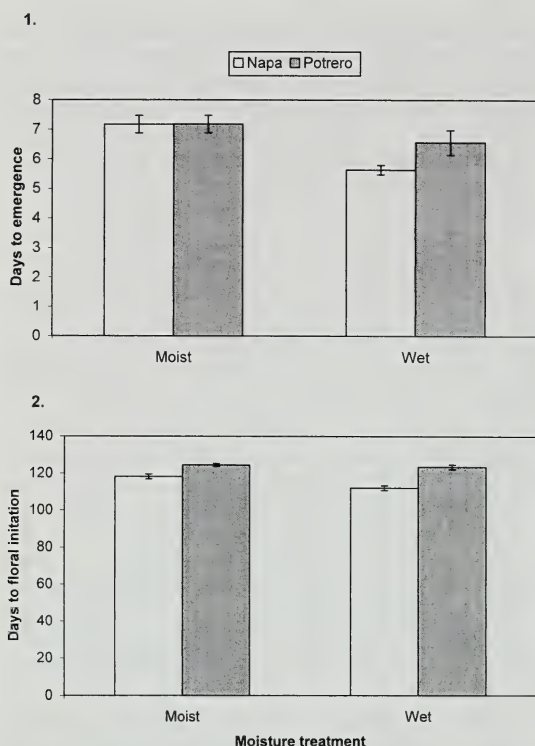
FIGS. 1–2. Performance of *L. conjugens* seeds and seedlings from two source populations subjected to two moisture treatments. Means ± SE are shown. **1.** Days to emergence. **2.** Days to floral initiation.
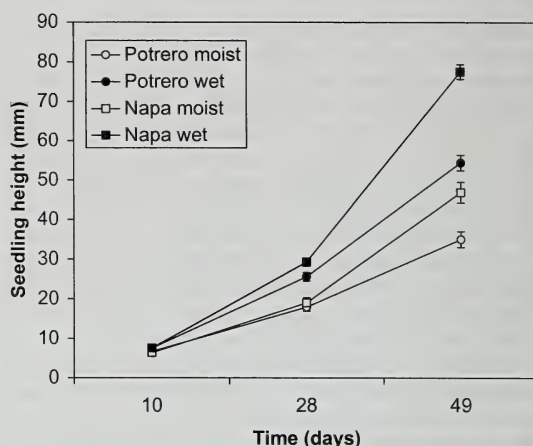

FIG. 3. Heights of *L. conjugens* seedlings over the first seven weeks of the soil moisture experiment in relation to source population and moisture treatment. Means ± SE are shown.

Soil Salinity Experiment

Seed germination in the salinity experiment was generally high for seeds from the Napa and Travis populations, and lower for seeds from the Potrero population (Table 4). Increasing salinity reduced the proportion of seeds germinated for both the Travis and Potrero population, but not for the Napa population. Floral initiation followed a similar pattern, with fewer plants initiating flowers at the highest salinity treatment (Table 4). Seedling mortality

was equivalent across salinity treatments for the Napa and Potrero populations, and was slightly, but not significantly higher for the Travis population at intermediate and high salinity levels (Table 4).

For seeds that germinated, both source population and salinity treatment influenced time to emergence (Fig. 4, nested ANOVA, treatment*population interaction, $F_{6,6} = 2.97$, P = 0.008). This result paralleled the overall pattern for germination and floral initiation, noted above. Seedling emergence time for the Potrero, but not the Napa and Travis populations, depended significantly upon salinity treatment. In particular, seeds from the Potrero population took much longer to germinate under the highest salinity treatment than did seeds from the other two populations (Fig. 4). Additionally, seeds from the Potrero population in the control treatment germinated significantly more slowly than those from the Travis population in the 5 ppt salinity treatment (Tukey-Kramer test, P < 0.05, Fig. 4) and seeds from the Potrero population in the highest salinity treatment

TABLE 2. RESULTS OF NESTED ANOVA ON TIME TO EMERGENCE, TO INITIATE FLOWERS, AND TO FLOWER FOR *L. CONJUGENS* PLANTS FROM THE POTRERO AND NAPA POPULATIONS SUBJECTED TO TWO MOISTURE TREATMENTS. Populations were analyzed separately. Degrees of freedom = 1 for treatment effect and 6 for Tray[Treatment] effect. No plants flowered from the Potrero population. [a] Tray[Treatment] effect could not be estimated due to low sample sizes.

Source of variation	Time to emergence		Time to initiate flowers[a]		Time to flower[a]	
	F	P	F	P	F	P
Potrero						
Treatment	5.47	<0.05	1.42	>0.20	N/A	N/A
Tray[Treatment]	8.79	<0.01	N/A	N/A	N/A	N/A
Napa						
Treatment	15.85	<0.01	12.96	<0.01	0.25	>0.50
Tray[Treatment]	2.48	<0.05	N/A	N/A	N/A	N/A

TABLE 3. RESULTS OF NESTED, REPEATED MEASURES AN-OVA ON HEIGHTS OF *L. CONJUGENS* SEEDLINGS MEASURED AT 10 D, 4 WK, AND 7 WK AFTER GERMINATION IN RESPONSE TO MOISTURE TREATMENT (MOIST OR WET) FOR EACH SOURCE POPULATION (POTRERO OR NAPA). We report ad-justed univariate values because data did not meet the sphericity assumption (SAS 2001).

Source of variation	F	P
Potrero		
Time	194.36	<0.001
Time × Treatment	13.59	<0.001
Time × Tray[Treatment]	0.95	>0.25
Napa		
Time	432.22	<0.001
Time × Treatment	33.54	<0.001
Time × Tray[Treatment]	1.79	>0.05

germinated more slowly than seeds in all other treat-ments (Tukey-Kramer test, P < 0.05, Fig. 4).

Salinity hindered seedling growth in a similar manner for plants from all three source populations (nested ANOVA, significant time*treatment inter-action; non-significant time*treatment*population interaction, Table 5). For all three populations, seedlings grew fastest in the control treatment and slowest in the 20 ppt salinity treatments (Fig. 5, Table 5).

DISCUSSION

Lasthenia conjugens germination, growth, devel-opment, and seedling mortality were significantly affected by the soil moisture and soil salinity treat-ments that we imposed, and the nature of seedling response to these treatments often depended upon the population from which the seeds were collected. For example, we observed significant declines in seedling performance in relation to soil salinity, but this effect was strongest for seeds from the Potrero population. Because plants from certain populations may respond differently to soil moisture and soil salinity than plants from other populations, source population should be an important consideration in

design of *L. conjugens* reintroduction to restored sites.

Soil Moisture Experiment

For both populations examined in the moisture experiment, soil moisture treatment significantly af-fected germination, timing of development, and seedling growth rates. Seeds from the Potrero pop-ulation had higher germination under moist condi-tions than wet conditions, yet grew more quickly in wet conditions. Seeds from the Napa population, however, germinated more often, and seedlings grew more quickly and were more likely to flower under wet conditions than under moist conditions. Interestingly, seedling mortality was higher in moist conditions than in wet conditions for seed-lings from both populations. Distinct patterns of be-tween-pool and between-site vernal pool plant abundance have been attributed to variation in soil moisture or duration of inundation (Holland and Jain 1984; Martin and Lathrop 1986; Zedler 1987). In this experiment we directly manipulated soil moisture and observed significant plant growth re-sponses, but did not directly test the effect of in-undation on *L. conjugens* performance. Ongoing greenhouse experiments explicitly examine the consequences of variable inundation schemes for *L. conjugens* germination, growth, and survival (Ger-hardt and Collinge unpublished data) and will be reported elsewhere.

Overall germination rates for *L. conjugens* seeds were relatively high (>65%) in the moisture ex-periment. There have been no suggestions of com-plex seed dormancy mechanisms in this species or its congeners (Crawford and Ornduff 1989), and it appears that ample soil moisture conditions are suf-ficient to elicit *L. conjugens* germination. However, seedling mortality was high (57–90%), particularly for plants in low soil moisture conditions. Thus, it appears that low soil moisture may limit seedling lifespan and reduce the potential for these annual plants to complete development and produce viable seeds.

We examined the effect of maternal family on

TABLE 4. SEED GERMINATION, FLORAL INITIATION, AND MORTALITY IN THE SALINITY EXPERIMENT. N = 100 seeds planted per population and treatment, for a total of 1200 seeds. Ppt is parts per thousand of synthetic sea salt in tap water. Germination percent is calculated as the number germinated divided by the number planted (100). Percent floral initiation and percent mortality (in parentheses) are calculated as the number of individuals in that category divided by the number of individuals that germinated. [a] $\chi^2_{[6]}$ = 27.5, P<0.001. [b] $\chi^2_{[6]}$ = 19.9, P<0.01. [c] $\chi^2_{[6]}$ = 12.0, P=0.07.

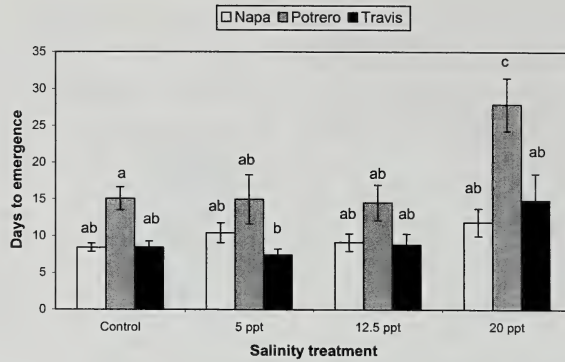| Popu-lation	Germination[a] (%) Salinity treatments				Floral initiation[b] (%) Salinity treatments				Mortality[c] (%) Salinity treatments			
	Control	5 ppt	12.5 ppt	20 ppt	Control	5 ppt	12.5 ppt	20 ppt	Control	5 ppt	12.5 ppt	20 ppt
Napa	71	64	76	65	52 (73.2)	23 (35.9)	25 (32.8)	14 (21.5)	19 (26.7)	14 (21.9)	16 (21.1)	19 (29.2)
Travis	61	68	71	19	25 (41.0)	30 (44.1)	18 (25.3)	4 (21.1)	7 (11.5)	15 (22.1)	21 (29.6)	5 (26.3)
Potrero	45	28	29	15	23 (51.1)	8 (28.5)	3 (10.3)	1 (6.7)	10 (22.2)	10 (35.7)	11 (37.9)	9 (60.0)

Fig. 4. Days to emergence for *L. conjugens* seeds from three source populations subjected to three salinity treatments, plus a control treatment. Ppt refers to parts per thousand of synthetic sea salt. Means ± SE are shown. Means with different letters are significantly different from one another.

seedling growth for seeds from the Potrero population in the moisture experiment. Even after accounting for differences due to moisture treatment, we observed two-fold differences in seedling height at seven weeks among maternal families. We collected seeds within a 4-ha area of the Potrero Hills site from plants ranging in distance from only 1–100 m apart. These results are consistent with many studies showing that maternal parent can have large fitness-related consequences for offspring (Antonovics and Schmitt 1986; Mazer and Gorchov 1996; Dudash et al. 1997) and suggest that restoration efforts should carefully consider seed sources to be used for reintroduction. We suggest that seed collection should include numerous maternal families from sites in order to represent the full range of genetic variation present (e.g., Lesica and Allendorf 1999).

Soil Salinity Experiment

Germination rates ranged more widely (15–76%) in the salinity experiment than the moisture experiment, and were negatively related to salinity treatment for the Potrero and Travis populations (15 and 19%, respectively) but not for the Napa population (65% germination). This result suggests that high salinity may reduce the number of seeds that ger-

minate within a population, but that it may depend on the particular population.

Our observed differences in overall germination among the three populations cannot necessarily be attributed to inherent differences among these populations. Seeds from the three populations were collected in different years and were stored under slightly different conditions, which may have influenced their viability. Because we mixed seeds from each population before assigning them to salinity treatments, however, we are confident that the differences in germination that we observed among treatments represent significant biological responses of the plants from different populations to soil salinity.

Because of observed variation in *L. conjugens* abundance at sites that experience variable historical and current soil salinity conditions (Dains 1995;

TABLE 5. RESULTS OF NESTED, REPEATED MEASURES ANOVA ON HEIGHTS OF *L. CONJUGENS* SEEDLINGS MEASURED AT 14 D, 28 D, AND 43 D AFTER GERMINATION IN RESPONSE TO SALINITY TREATMENT AND SOURCE POPULATION. We report adjusted univariate values because data did not meet the sphericity assumption (SAS 2001).

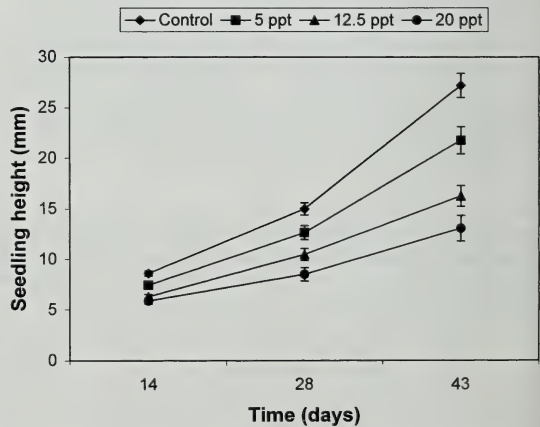| Source of variation	F	P
Time	170.54	<0.001
Time × Treatment	10.78	<0.001
Time × Tray[Treatment]	1.00	>0.10
Time × Population	1.21	>0.10
Time × Population × Treatment	0.44	>0.50

Fig. 5. Heights of *L. conjugens* seedlings over the first six weeks of the soil salinity experiment in relation to soil salinity treatment. Data were combined for all three source populations because the populations did not differ significantly from one another in their growth response to the salinity treatments. Means ± SE are shown.

Vollmar 1997; Collinge personal observation), we expected that high salinity would hinder germination and growth. Plants from all three populations performed more poorly under high salinity conditions than low salinity conditions, but the Potrero population was more strongly negatively affected by high salinity than the other two populations (Table 4). This result was unexpected, given that it is likely that the Potrero population historically and currently experiences the most saline conditions of the three populations, and is contrary to our initial prediction that there may be local adaptation to soil salinity for plants from the Potrero population. We conclude from our results that seedlings from these three populations do differ in response to soil moisture and salinity. Because we sampled only one population at each point along a salinity gradient, however, we do not have the statistical power to infer that these differences are due to the salinity conditions of the populations from which we collected the seeds.

Soil salinity and alkalinity are often quite variable in space and time, and are clearly important components of germination and performance of many plant species that occur in temporary or permanent wetlands (e.g., McLaughlin 1974; Kingsbury et al. 1976; Ungar 1978, 1995; Khan and Ungar 1984; Charpentier et al. 1998; Noe and Zedler 2000). For example, Noe and Zedler (2000) reported significant inhibition of seed germination under experimentally induced high salinity conditions in several annual salt marsh species, including *Lasthenia glabrata* subsp. *coulteri,* a congener of *L. conjugens.* Interestingly, for many species the response to salinity depended upon the amount of soil moisture to which the plants were exposed (Noe and Zedler 2000). In our experiment we manipulated soil salinity and soil moisture separately, but did not examine interactions between moisture and salinity. Further, we did not directly manipulate soil alkalinity. Because soil moisture, salinity and alkalinity vary across the geographic range of *L. conjugens,* it would be useful to conduct further experiments to directly examine the interactive effects of these environmental factors on plant performance.

The degree of local adaptation to environmental conditions may depend significantly on the spatial scale at which environmental variation occurs and at which plants respond. For example, in recent studies of another rare annual herb in California, *Lupinus guadalupensis* (Guadalupe Island lupine, Fabaceae) Helenurm (1998) detected no local adaptation among source populations located 10 km apart and that differed in vegetation community, dominant species, soil type, and parent material. Helenurm (1998) suggested that perhaps local adaptation might be uncommon on fine spatial scales (≤10 km), where environmental differences among sites may be less pronounced than at broader scales. In contrast, prior work on vernal pool plants re-

vealed genetic differentiation among plants located 2–5 meters apart within vernal pools (Linhart 1974, 1976, 1988; Linhart and Baker 1973). For *L. conjugens,* populations separated by short distances may exhibit striking gradients in soil salinity and alkalinity (Dains 1995; Vollmar 1997), which may impose strong selection that promotes genetic differentiation and local adaptation. Clearly, further research should explore the extent to which genetic differentiation and local adaptation occur in vernal pool plant species, given its potential importance for restoration and reintroduction efforts.

Conclusions

In summary, our results support several conclusions regarding *L. conjugens* seed germination and seedling ecology, which have important implications for conservation and restoration of *L. conjugens* populations and further contribute to our understanding of vernal pool plant response to variation in abiotic environmental conditions. First, the fact that *L. conjugens* seeds germinate readily in response to moist soil conditions should facilitate population reintroduction. Limited understanding of germination requirements should not hinder reintroduction of new populations under suitable physical conditions. Germination may be inhibited, however, under high salinity conditions, even for seeds collected from historically or currently saline sites. The negative germination response to high salinity that we observed suggests the need for further investigation of germination responses of *L. conjugens* plants from salt-marsh sites, such as the San Francisco National Wildlife Refuge.

Second, moisture and salinity treatments did result in environments different enough to affect the responses of *L. conjugens* seeds and seedlings in our experiments. Year-to-year variation in rainfall, soil salinity, and inundation of individual pools may strongly affect the success of *L. conjugens* individuals. Our results suggest that fully saturated, low salinity soils may provide excellent conditions for germination and early growth of *L. conjugens.*

A third important result from our study is that seed source may critically influence the viability of plants in a given environment. Seeds collected from the three populations may have selectively important differences related to germination and growth requirements. Such local differentiation in plant populations has been reported for a variety of species (Farris 1987; reviewed in Linhart and Grant 1996). Our observed differences in performance and response to environmental conditions based on source population and maternal family underline the importance of carefully considering source locations and collection schemes for restoration and reintroduction efforts (Elam 1998; Havens 1998; Lesica and Allendorf 1999). We suggest that seed collections for vernal pool restoration should come from existing pools at or near the same site where

restoration will occur, and should contain a variety of maternal plant families.

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DOMACIOS FOLIARES EN DOS ESPECIES DE *TERMINALIA* (COMBRETACEAE)

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ABSTRACT

Exomorphic and anatomical descriptions of leaves with domatia of two *Terminalia* species are given. Crypt-type domatia covered by trichomes were found in *Terminalia triflora* (Griseb.) Lillo and *T. australis* Cambess. They occur at the junction of primary and secondary veins, on the leaves abaxial surface. A key to the two species is provided.

RESUMEN

Se describe la exomorfología y la anatomía de hojas con domacios en dos especies de *Terminalia* (Combretaceae). Los domacios se ubican en las axilas de las venas primaria y secundarias, en la cara abaxial de las hojas. Ambas especies de *Terminalia*, *T. triflora* (Griseb.) Lillo y *T. autralis* Cambess., presentan domacios foliares del tipo "en criptas" frecuentemente cubiertos por mechones de pelos. Se presenta una clave para facilitar la identificación de ambas especies.

Palabras Claves: Morfología, anatomía, domacios foliares, criptas, mechones de pelos, *Terminalia*.
Key Words: Morphology, anatomy, leaf domatia, crypts, trichomes, *Terminalia*.

Los domacios son estructuras que varían desde pasajes cavernosos en rizomas, tallos o pecíolos a diminutos huecos o mechones de pelos en la superficie abaxial de las hojas, los llamados domacios foliares (Stace 1965). Estas estructuras, que pueden servir de abrigo a pequeños animales que viven en simbiosis con las plantas, varían en incidencia, grado de desarrollo, forma y con las condiciones ambientales, en y entre individuos de la misma variedad y especie (Pemberton and Turner 1989). Tanto la presencia como el tipo de domacio han sido utilizados para caracterizar géneros o distinguir especies dentro de ellos (Metcalfe and Chalk 1979; Cerana y Ariza Espinar 1995).

Para la familia Combretaceae, se ha señalado la presencia de domacios "en bolsillo", "en mechones de pelos" o "en cripta", en numerosos géneros (Brouwer and Clifford 1990). Ferreira da Silva and Valente (1980) presentan un cuadro comparativo utilizando tanto la epidermis foliar como el tipo, morfología y ubicación de los domacios para interpretar algunos géneros de la familia Combretaceae del Estado de Río de Janeiro (Brasil). Citan a cuatro especies de *Terminalia* L.: *T. januarensis* DC. y *T. glabrescens* Mart. con domacios "en mechones de pelos" ubicados en las axilas de las venas primarias y secundarias; *T. brasilensis* (Cambess.) Eichl. y *T. acuminata* (Fr. Allem.) Eichl. con domacios en forma de "V", o bolsas con pelos en la abertura del mismo, ubicados en las venas primarias, secundarias o terciarias. Stace (1965) describió diferentes tipos de domacios en esta familia. Para el género *Terminalia* mencionó los marsupiformes y lebetiformes. Gauglianone (1998) cita la presencia de domacios fasciculados en el envés de las hojas de *Ter-*

minalia. Las especies analizadas en este trabajo, *T. triflora* (Griseb.) Lillo y *T. australis* Cambess., no fueron estudiadas anatómicamente por estos autores.

MATERIALES Y MÉTODOS

Se analizó material vivo en diferentes estados de desarrollo, el que fue fijado en FAA (Formol–Ácido acético–Alcohol 96°) y material seco, previamente hidratado por hervor con agua jabonosa. Los ejemplares de respaldo se encuentran depositados en el Herbario del Instituto de Botánica del Nordeste, (CTES).

Para la descripción anatómica se realizaron preparaciones permanentes. Se utilizaron deshidratantes histológicos y la preimpregnación se llevó a cabo con aclarante preimpregnante (González y Cristóbal 1997). Para la infiltración en parafina se utilizó la técnica de Johansen (1940), posteriormente se incluyeron en "Histoplast". Los cortes se realizaron con micrótomo rotativo, desde el extremo proximal al extremo distal de los domacios, en un espesor que osciló entre 12 y 15 μm, se tiñeron con safranina-astra blue (Luque et al. 1996) y montaron en bálsamo de Canadá sintético.

El material fue diafanizado según la técnica de Dizeo de Strittmatter (1973) y teñido con safranina, para el análisis de la vascularización de las hojas. Se contaron los estomas y se obtuvieron los índices estomáticos, según la fórmula de Salisbury (Metcalfe and Chalk 1979). Para la descripción de la arquitectura foliar se ha seguido la terminología de Hickey (1974). Las observaciones y fotografías del material se efectuaron con microscopio esteroscópico Wild M5, microscopio óptico binocular Olym-

pus BX 50F y en microscopio electrónico de barrido JEOL 5800 LV a 20 kV. Para los dibujos se utilizó cámara clara. En los diagramas se usaron los signos convencionales de Metcalfe and Chalk (1957), los estomas se representaron con una "X".

Material Estudiado

Terminalia australis. **ARGENTINA.** *Provincia: Corrientes. Dpto. Santo Tomé,* Ea. Timbó, Potrero Luna, 5-XII-81, *Tressens et al. 1629* (CTES, 197098); *Dpto. San Martín,* Yapeyú, 28-I-76, *Krapovickas y Cristóbal 28991* (CTES, 197286); 6 km SW de La Cruz, sobre la costa del río Uruguay, 8-II-79, *Schinini et al. 16836* (CTES, 197092); *Dpto. Ituzaingó,* 10 km al W de San Carlos, 9-IX-78, *Cristóbal y Ahumada 1729* (CTES, 197278); *Dpto. Paso de los Libres,* Bonpland, Ea. El Recreo, sobre el río Uruguay, 12-XI-80, *O. Ahumada y Schinini 4006* (CTES, 197097); Paso Troncón, 8-XII-78, *Krapovickas y Cristóbal 34251* (CTES, 197287); *Dpto. Montes Caseros,* 8 km al S de Lobougle, costa del Río Uruguay, 22-II-79, *Schinini et al. 17596* (CTES, 197094). *Provincia: Misiones. Dpto. Guaraní,* Predio Guaraní, arroyo Soberbio, 3-XI-99, *Tressens et al. 6513* (CTES, 318851); *Dpto. Montecarlo,* Arroyo Isla, 3 km al S del puente sobre ruta N° 15, 28-XII-01, *Keller 505* (CTES, 327713); *Dpto. San Pedro,* Parque Provincial Moconá, 29-XI-93, *Seijo et al. 848* (CTES, 238031); *Dpto. Gral. Belgrano,* Propiedad Los Palmitos de Alto Paraná S.A., sobre ruta N° 227, 13-XI-99, *Keller 105* (CTES, 317674). *Provincia: Buenos Aires. Dpto. Zárate,* Ea. Las Palmas, barrancas del Paraná, 13-XI-67, *Boelcke et al. 13162* (CTES, 240702); Isla Martín Garcia, Selva Oriental Norte, 3-XI-93, *Hurrell 1525* (CTES, 238060). **BRASIL.** Barra do Quaraí, beira do rio Quaraí, no bosque do declive E do ponte internacional, 1-X-71, *Linderman 8443* (CTES, 197285); Eneas Marques, Paraná, 11-X-74, *Hatschbach 35171* (CTES, 197276).

Terminalia triflora. **ARGENTINA.** *Provincia: Corrientes. Dpto. Ituzaingó,* río Aguapey y Ruta 38, 4-XII-80, *Tressens 1170* (CTES, 195485); *Dpto. Capital,* Molina Punta, 3-XII-93, *Tressens y Solís 4764* (CTES, 222464); Is. Meza, 19-I-94, *Solís Neffa 14* (CTES, 230507); Perichón, costa del río Paraná, 18-12-00, *Schinini 35248* (CTES, 328508); *Dpto. San Cósme,* orilla del río Paraná, 8-X-72, *Krapovickas y Cristóbal 22251* (CTES, 214292); Paso de la Patria, 1-I-98, *Franceschini 16* (CTES, 301581); 6 km al E de Paso de la Patria, orilla del río Paraná, 30-IX-87, *Krapovickas y Schinini 41912* (CTES, 214297); *Dpto. Paso de los Libres,* Ea. "El Recreo", 21 km E Bonpland costa río Uruguay, 18-XI-73, *Lourteig et al. 2755* (CTES, 214288). *Provincia: Chaco. Dpto. San Fernando,* Isla Soto, 28-XI-78, *Schinini 16142* (CTES, 214337); *Dpto. 1° de Mayo,* Colonia Benítez, 13-IX-78, *Schulz 16027* (CTES, 214311). *Provincia: Misiones. Dpto. Candelaria,* Prefectura Naval Ar-

gentina, costa del río Paraná, 5-5-97, *Tressens et al. 5741* (CTES, 281002); *Dpto. Iguazú,* Parque Nacional Iguazú, Isla San Martín, 15-X-93, *Tressens et al. 4564* (CTES, 222449). *Provincia: Salta. Dpto. Anta,* Parque Nacional "El Rey", 24-XI-81 *Brown y Malmierca 1700* (CTES, 214334); *Dpto. Santa Victoria,* camino del Condado a Los Toldos, 6-X-73, *Legname y Cuezzo 9605* (CTES, 214320). *Provincia: Formosa. Dpto. Capital,* Ea. "Guaycolec", 25 km N de la ciudad de Formosa, ruta Nac. N° 11, 10-10-89, *Placci y Arditi 131* (CTES, 214328); *Dpto. Pilcomayo,* El Paraiso en selva, 4-X-81, *Valla et al. 17656* (CTES, 214300). **PARAGUAY.** *Dpto. Paraguarí,* Cerros Palacios, 13-IX-91, *Degen 2079* (CTES 264940); *Dpto. Amambay,* Bella Vista, río Apa y arroyo Estrella, 25-XII-80, *Schinini y Bordas 20689* (CTES, 214332); *Dpto. Concepción,* Rancho Esperanza, 21-X-91, *Degen 2158* (CTES, 219926); *Dpto. Capital,* Puerto Itá Enramada, 6-IX-76, *Schinini 13351* (CTES, 214305); *Dpto. Caazapá,* distribuidora Yuty a 15 Km al S de Capitindy, 10-IX-87, *Arbo et al. 2846* (CTES, 214321). **BRASIL.** Joaquim Tavora, arredores, Paraná, 30-XI-76, *Hatschbach 39279* (CTES, 357332); río Bandeirantes (Mun. Santa Fé) Paraná, 1-IX-89, *Silva & Hatschbach 650* (CTES, 230201); río Guaviral (Mun. Bela Vista) Mato Grosso do Sul, 23-X-87, *Hatschbach & Silva 51597* (CTES, 214327).

RESULTADOS

Terminalia triflora

Exomorfología de la hoja: entera, con pelos simples, erectos, curvos y adpresos (Fig. 1E); limbo angosto, latielíptico u obovado-elíptico; margen entero; ápice truncado, emarginado o agudo; base aguda; venación pinnada, camptódroma, broquidódroma, vena primaria con recorrido recto, venas secundarias de cuatro a siete pares curvados, ángulo de divergencia casi uniforme, 40°–50°, aréolas con disposición al azar (Fig. 1F, G).

Anatomía de la hoja: *Epidermis adaxial* uniseriada; con células poligonales, paredes delgadas, rectas o levemente sinuosas; cutícula bien desarrollada. *Mesofilo* de estructura dorsiventral; haces vasculares colaterales cerrados, rodeados de células esclerenquimáticas unidas a la epidermis por células parenquimáticas; abundantes idioblastos con drusas de tamaño variable. *Epidermis abaxial* uniseriada, células de igual tamaño que las de la epidermis superior; cutícula gruesa, estomas anomocíticos (Fig. 1C, H), índice estomático de 16 a 18%. *Vena media* formada por un haz colateral abierto rodeado de fibras; por arriba y por debajo del haz se ubican pequeñas cantidades de tejido colenquimático, separadas del esclerénquima por células parenquimáticas; abundantes idioblastos con drusas y cristales prismáticos de tamaño variable.

Descripción del domacio: los domacios se ubican en el hipofilo a lo largo de la vena media, en la axila
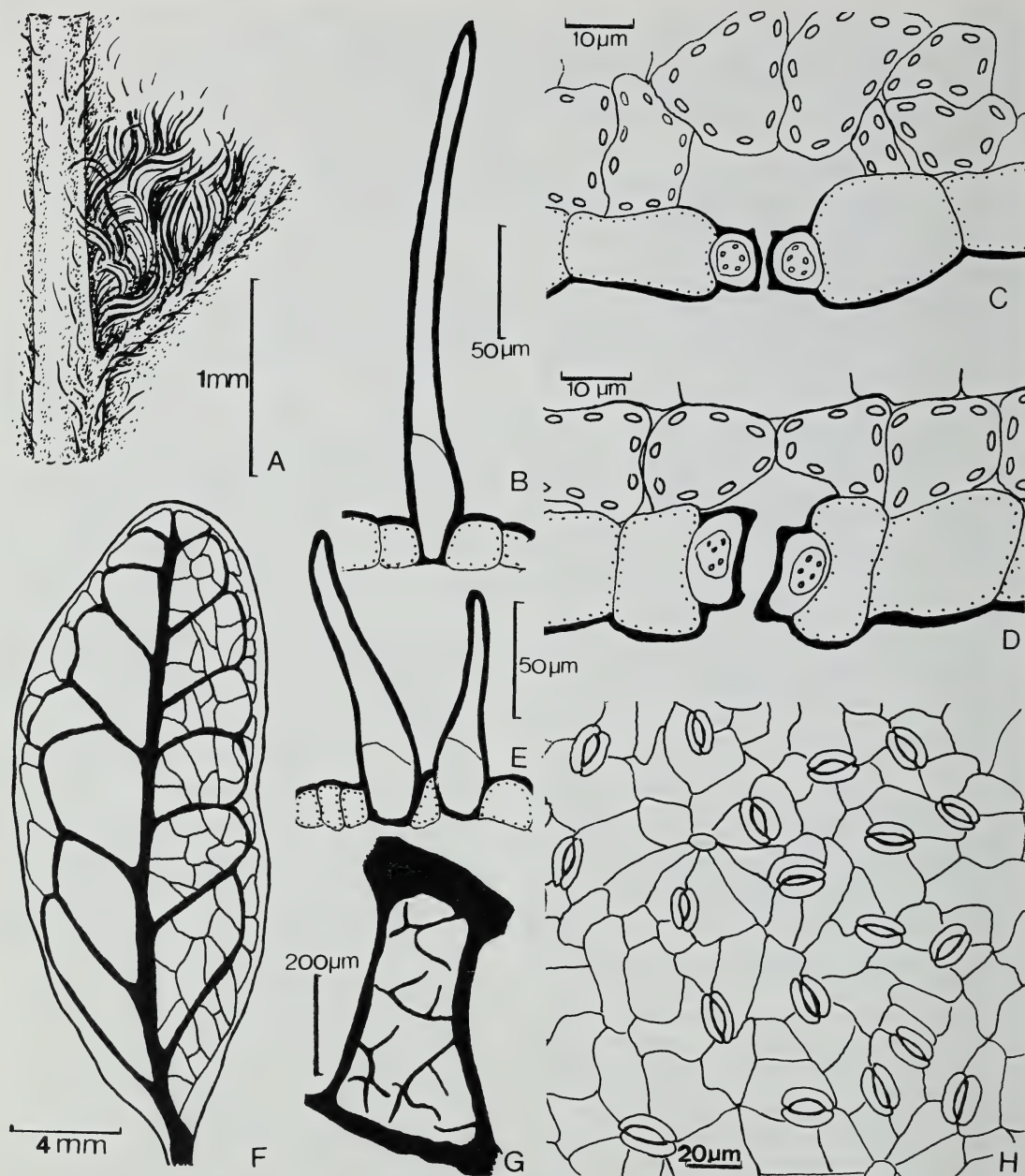
FIG. 1. Morfología foliar de *Terminalia triflora*. **A,** domacio; **B,** pelo simple de la epidermis del domacio; **C,** corte transversal de un estoma de la epidermis abaxial de la lámina; **D,** transcorte de un estoma de la epidermis del domacio; **E,** pelo simple de la epidermis abaxial de la lámina; **F,** venación; **G,** detalle de una aréola; **H,** epidermis abaxial de la lámina. (*Tressens y Solís, 4764*).

de las venas secundarias, donde se observan como mechones de pelos; disminuyen de tamaño hacia el ápice foliar y su número varía en cada hoja; en las adultas se presentan entre 4 ó 5 domacios. Estas estructuras son constantes en la especie (Figs. 1A, y 2A). El domacio forma una depresión cuya profundidad varía en las diferentes hojas. Con fines des-

criptivos se denomina extremo proximal del domacio al ángulo que forma la vena secundaria con la vena media, y extremo distal al área donde ya no se observa ni depresión ni acumulación de pelos. Se observó la siguiente secuencia:

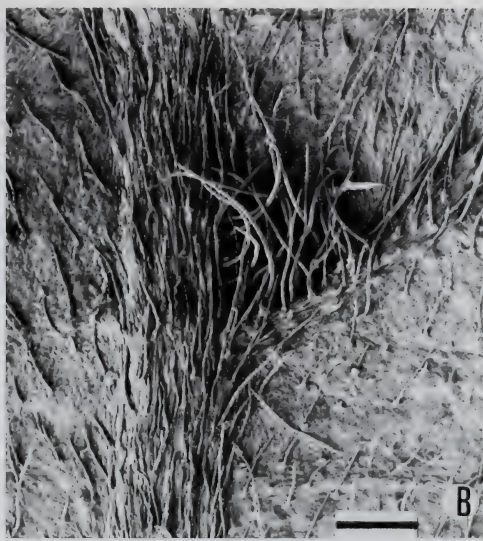- El tejido clorenquimático es desplazado hacia

FIG. 2.   Vista superficial de domacios en *Terminalia*. **A,** *T. triflora* (*Tressens, 1170*); **B,** *T. australis* (*Krapovickas y Cristóbal, 28991*). Escala indica: 200 μm.

la cara adaxial de la hoja por la presencia de un tejido parenquimático sin cloroplasto, que se continúa desde la vena media (Fig. 3A, E).

- Se observa el inicio de la cripta como una leve depresión (Fig. 3B, F), donde las células epidérmicas, de forma rectangular y poco cutinizadas, presentan estomas y pelos simples (Fig. 1D, B).
- La cripta se va haciendo más grande y profunda, hasta tomar en sección forma de "V"; la epidermis sigue siendo uniestratificada con células pequeñas, todas de igual tamaño (Fig. 3C, G). Ya no se observa el parénquima incoloro y clorénquima, se forma un mesofilo bien desarrollado que constituye el "piso". Presenta haces vasculares pequeños.
- La cripta progresivamente se hace menos cóncava (Fig. 3D, H).

En algunas hojas se observó una estructura algo diferente (Fig. 4A–H), debido a que en el extremo proximal el domacio se inicia como un canal que se abre al exterior en la cripta. Dicho canal consta de un "piso" y un "techo". El piso está constituido por clorénquima y el techo por células parenquimáticas incoloras (Fig. 4B, F). La cripta está tapizada por células epidérmicas que constituyen la "epidermis del domacio", en la misma se observan estomas y pelos simples (Fig. 4C, D, G, H). Se presentan numerosos idioblastos, con drusas distribuidos irregularmente en el mesofilo de la lámina.

Terminalia australis

No se incluye la descripción morfológica y anatómica de la hoja, debido a que prácticamente no se encontraron diferencias con la de *T. triflora*.

Descripción del domacio: En esta especie se presentan zonas pubescentes o pilosas, en las axilas de las venas secundarias basales, sólo en algunas hojas bien desarrolladas (Fig. 2B). También se han observado numerosos ejemplares en los que estas estructuras están ausentes.

Estos domacios se constituyen tardíamente en las hojas. No son constantes y están reducidos a uno o dos por lámina. En los ejemplares con domacios, se puede observar, en la separación de la vena primaria con la secundaria, una pequeña depresión que abarca el tejido epidérmico inferior y parte del mesofilo. Esta depresión esta tapizada por una reducida cantidad de pelos simples y de estomas. Esto se interpreta como domacio "en cripta", generalmente poco profunda. No produce alteración ni rotura del tejido foliar (Fig. 5A–D).

DISCUSIÓN Y CONCLUSIONES

Stace (1965) denomina domacios lebetiformes ("bowl-shaped") a las depresiones en la superficie foliar, que generalmente se encuentran en las axilas de las venas. Las mismas varían mucho en profundidad y las aberturas pueden presentarse de diferente forma y tamaño. Este autor considera diferentes grados de domacios lebetiformes en Combretaceae, según su profundidad; menciona el género *Lumnitzera* con un domacio muy simple, poco profundo, como lo observado en el presente trabajo en algunas hojas de *Terminalia australis*.

El mismo autor (1965) describe a los domacios en mechones de pelos o fasciculados ("tufts of hairs"), como zonas pubescentes o pilosas en las axilas de las venas de las hojas, sin otra modificación que el desarrollo de pelos.

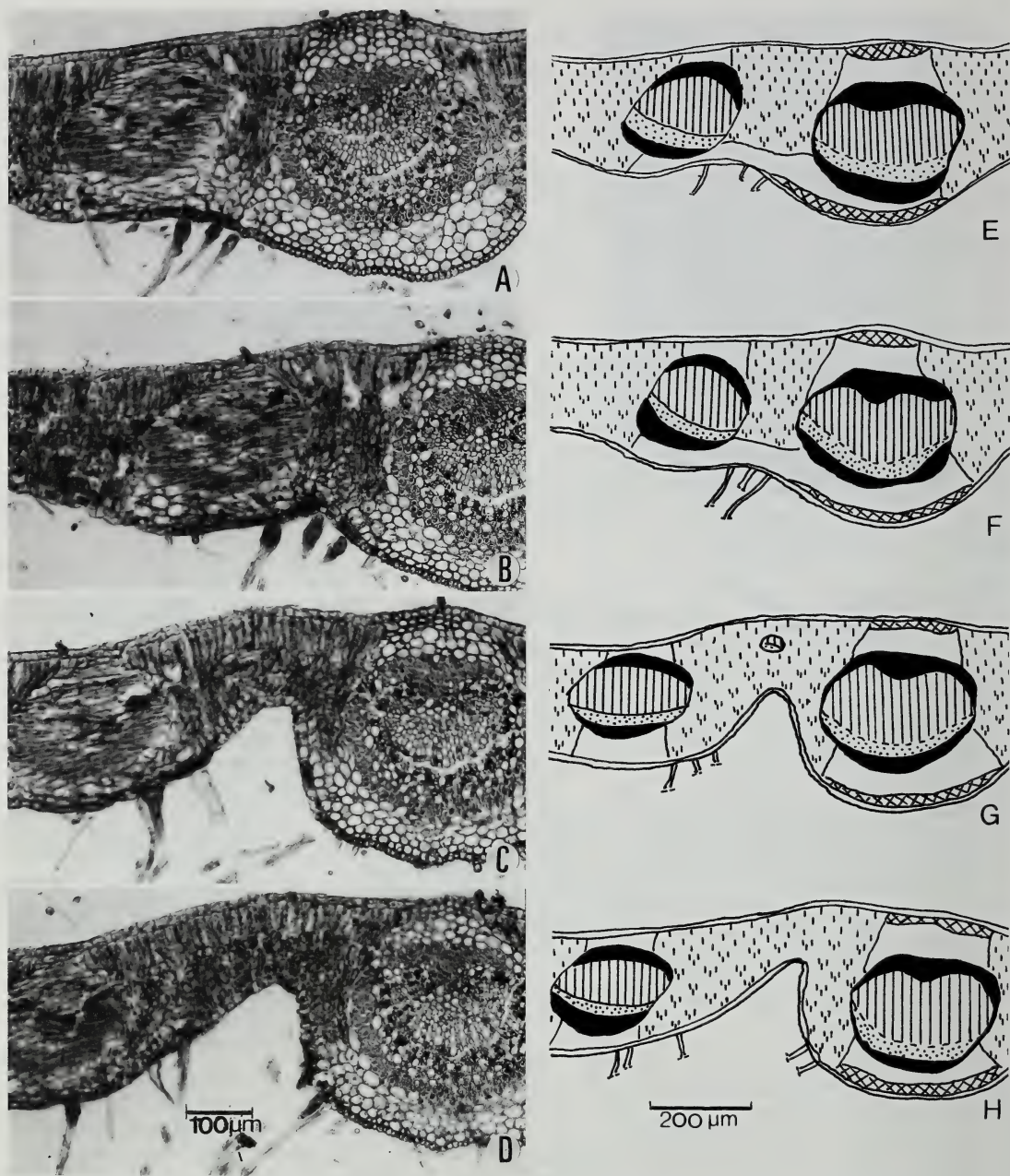Guaglianone (1998) describe a los domacios de

Fig. 3. Anatomía del domacio de *Terminalia triflora*. **A–D,** fotomicrografías de secciones tranversales del domacio "en cripta"; **E–H,** representación esquemática de las secciones fotografiadas en A–D (*Tressens y Solís, 4764*).

Terminalia como "fasciculados", y señala que están presentes en *T. triflora* y generalmente ausentes en *T. australis*. Según el estudio anatómico, los domacios presentes en estas dos especies; que aparentan ser "fasciculados", son en realidad del tipo "en cripta o lebetiforme" donde la concavidad varía en profundidad y el canal, cuando existe, en diámetro.

Para Jacobs (1965) la importancia taxonómica de los domacios es bastante controvertida, pero la regularidad con que se presentan los domacios en las hojas de *T. triflora* y su presencia ocasional en *T. australis,* como también las diferencias en caracteres externos de los domacios de ambas especies, llevan a considerar a los domacios de valor taxonómico. Estas especies presentan características morfológicas similares y cuando se carece del fruto
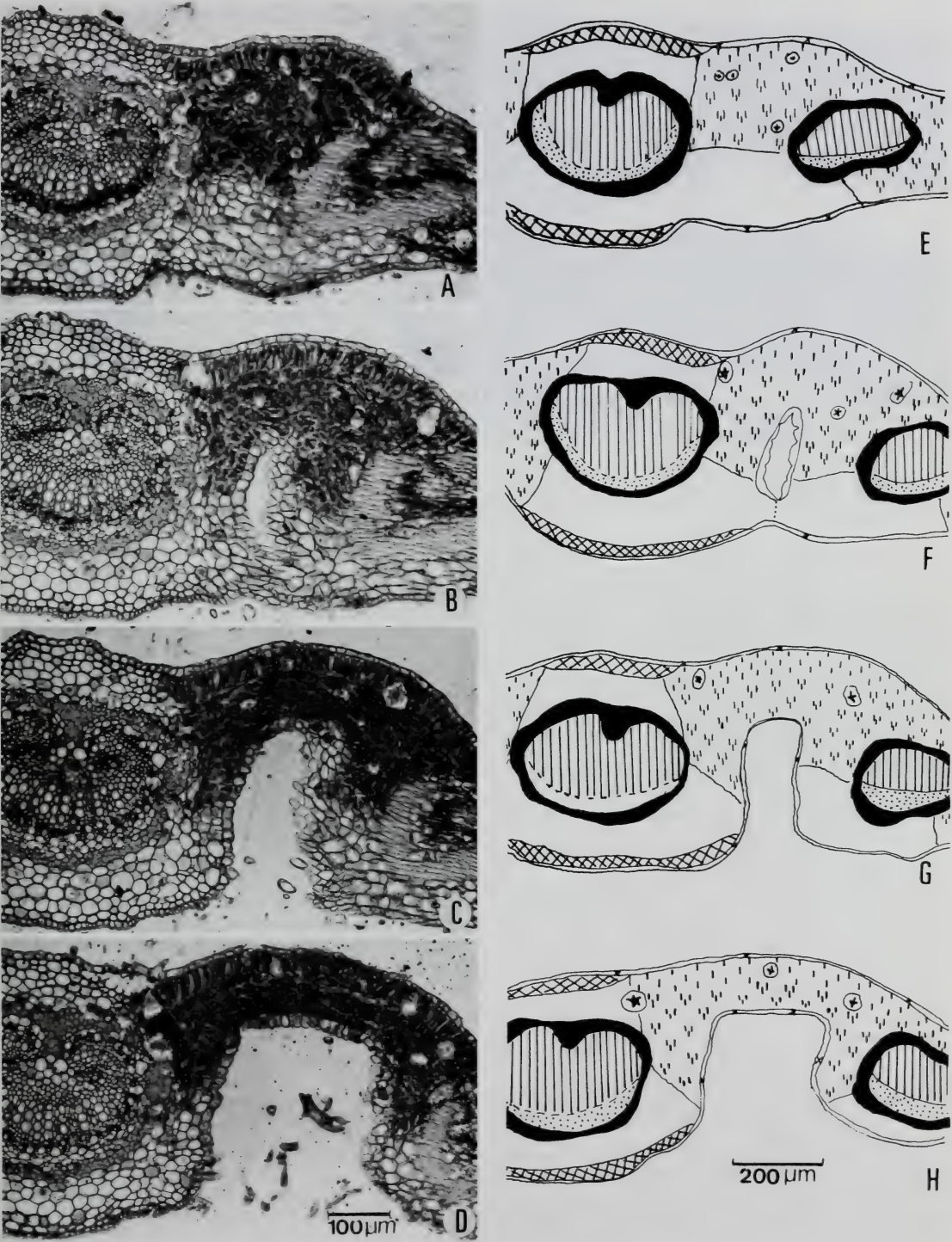
FIG. 4. Anatomía del domacio de *Terminalia triflora*. **A–D,** fotomicrografías de secciones tranversales del domacio "en cripta" desde la base foliar hacia el ápice de la lámina foliar; **E–H,** representación de las secciones fotografiadas en A–D (*Tressens y Solís 4764*).
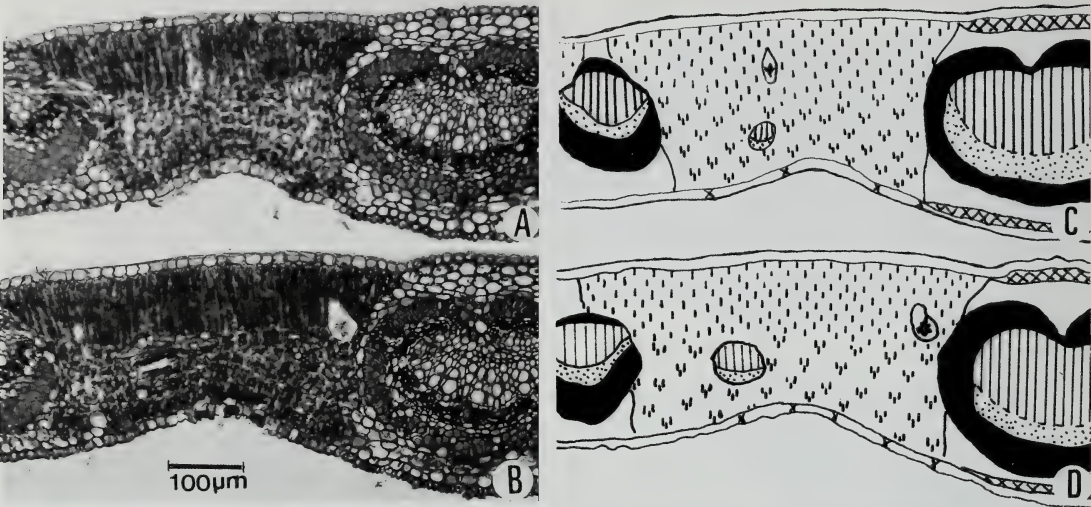
Fig. 5. Anatomía del domacio de *T. australis*. **A–B**: fotomicrografías de secciones transversales del domacio, **A,** extremo proximal, **B,** extremo distal; **C–D**, representación esquemática de las secciones fotografiadas en A–B (*Tressens et al. 1629*).

su identificación es difícil. Las diferencias encontradas que ayudarían a reconocer a las dos entidades aún en el caso del material estéril, se presentan en la siguiente clave:

a. Domacios "en cripta", con una concavidad profunda, excepcionalmente poco profunda, enmascarados por abundante cantidad de pelos, presentes en la mayoría de las hojas adultas, en número de 4 ó 5 por lámina foliar. Ocasionalmente domacios con canales internos . . . . *Terminalia triflora*
a'. Domacios "en cripta", con una concavidad poco o algo profunda, glabra o con una reducida cantidad de pelos, presentes en algunas hojas adultas, en número de 1 ó 2 por lámina foliar . . . . . .
. . . . *Terminalia australis*

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ASSESSING THE REPRODUCTIVE BIOLOGY OF
ERIASTRUM DENSIFOLIUM SUBSP. *SANCTORUM*
(SANTA ANA RIVER WOOLLY STAR, POLEMONIACEAE)

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ABSTRACT

This study assessed factors that affect reproductive success in *Eriastrum densifolium* subsp. *sanctorum* (*Eds*), a self-incompatible, endangered, perennial plant. We determined whether seed production was limited by resource allocation or pollinator activity and examined the influence of predation. The literature predicts that pollinator limitation in outcrossers would result if fruit set is less than 33%. We also used a regression analysis to examine the relationship between fruit set and resources or pollinator availability. Reproductive success of *Eds* appears to be both pollinator and resource-limited and was affected by predation. Mean fertilization success was high for Study Site One and low for the others. However, Site One had the lowest percentage of fertile seeds and the highest percentage of abortion. We conclude that pollinator limitation occurred up to seven seeds per capsule and above that level resource limitation predominated. *Eds* on Sites One and Five had the highest percentage of fertility and predation rates. Clearly, high predation may influence *Eds* population growth. Hummingbirds and the Giant Flower Loving Fly were the most common pollinators.

Key Words: Reproductive biology, resource limitation, pollinator limitation, predation, pollination ecology, Santa Ana Woolly Star, *Eriastrum densifolium* subsp. *sanctorum*.

Eriastrum densifolium subsp. *sanctorum* (Milliken) Mason, the Santa Ana River Woolly Star, (hereafter *Eds*), a member of the *Polemoniaceae*, is one of the 12 most endangered plants in California (York 1987). *Eds* is a self-incompatible perennial sub-shrub (Munoz 1991; Erickson 1993; Dorsett et al. 2000), that grows to approximately 25–75 cm in height (Munz 1974; Hickman 1993). It has leafy stems, dull gray-green leaves, and short branches. Flowers are clustered into bracteate floral heads that are terminal and lanate with corolla colors that range from lavender blue to purple, pink, or white and its throat and tube are generally yellow or white (Harrison 1972; Munz 1974; Hickman 1993). *Eds* is a distinct subspecies and is defined by corolla tube length, which is three times that of the calyx (Mason 1945; Brunell and Whitkus 1999a, b). In 1987, *Eds* was listed as an endangered subspecies under the Federal Endangered Species Act of 1973.

Several studies of *Eds* have been undertaken since 1987, and many of these have dealt with determining various aspects of the reproductive biology of this rare plant (see Dorsett et al. 2001 for a review of these studies). Qualitative observations seem to indicate that reproductive success in *Eds* may have declined over the past several years. We decided to attempt to determine if this apparent decline in fruit/seed set was related to either pollinator or resource limitation or was being affected by other factors such as predation.

There are many interrelated factors that may limit reproductive success in *Eds,* including (but not limited to) pollination limitation, resource availability, pollen quality, herbivory, genetic problems, and competition. Reproductive success is defined as the number of ovules that survive and mature into viable seeds that reproduce successfully (Wiens et al. 1987). Pollination limitation occurs when sufficient pollen to effect normal seed set has not been deposited on receptive stigmas (Lee 1988). Recent studies show that 62% or 258 wild plant species experienced pollinator limitation in at least one population per year (Burd 1994). Lee (1988) argues that, in many species from different habitats, fruit and seed will increase in supplementally pollinated plants if there is no resource limitation. Others who have studied the effects of increased pollen deposition on seed production indicate that seed number might increase, but seed quality may decrease (Galen and Newport 1988).

Resource limitation occurs when sufficient nutrients and photosynthates are not available to effect normal seed set and fruit production is limited as a result (Lee 1988). Lee (1988) further argues that in many species from differing habitats fruit and seed production is resource limited. Resources available to a given flower or fruit may vary from branch to branch and may be a function of the total number of reproductive structures drawing upon the resources. In addition, the number of reproductive structures requiring maternal investment of resources varies with time and with location on the individual because of uncertainties associated with pollination and seed production (Stephenson 1981).

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Given that there seems to be conflicting data re-garding whether resources or pollinators are more likely to limit fruit/seed production, it might be reasonable to assume that fruit/seed production within a given plant may be limited by pollinator availability during certain portions of the reproductive period and by resource availability during other portions.

Although the focus of the debate surrounding plant reproduction has been on pollinator versus resource limitation, Hendrix (1988) suggests that herbivores can reduce the success of plant reproduction by either preventing plants from entering the reproductive stage, or by the destruction of flowers, seeds, and fruits. Herbivores can affect both seed quality and seed number when vegetative tissues are damaged. Seed predation by insects is common, and is a major selective force that modifies many aspects of seed biology (Campbell 1985; Weiner 1988).

Genetic problems may also affect reproductive output. Bowers et al. (1981) and Wiens (1984) suggest that genetic problems can affect reproductive processes when low seed-ovule ratios in self-incompatible species may result from the accumulation of lethal and sub-lethal allelic combinations.

Competition in flowering plants can also affect fruit and seed production. Competition between species usually involves a deficit of space, nutrients, and/or other physical resources; flowering plants can also compete for pollinators. Such competition occurs when plants of one species experience a reduction in reproductive success because of sharing pollinators with another species (Campbell 1985). Weiner (1988) shows several possible results of competition, which affect reproductive behavior of plants.

Differentiating among the factors that limit reproductive success is often difficult because the factors are interrelated in a complex way. Determining what is responsible for the limitation of viable seed production requires a carefully designed study that focuses on experimental manipulation of a single factor such as pollen availability, resource limitation, or the effects of seed predation.

This study examines three factors (pollen availability, resource limitation, and predation), which may affect the reproductive biology of *Eds*. It is hypothesized that if there is pollinator limitation, the percent of fertile flowers will be less than 33% in a self-incompatible plant like *Eds*. Sutherland (1986) reviewed the fruit/flower ratios of many plant species and determined that self-incompatible species had a mean fruit/flower ratio of 33%. We examined the fruit/flower ratio in *Eds* with the expectation that if the ratio was higher than 33%, then pollinators were probably not limiting fruit production and conversely, if the ratio was lower than 33%, pollinators might be a limiting factor. To further examine whether reproduction in *Eds* is pollinator or resource limited, we examined the total

seed weight within a capsule as seed number within that capsule increases. If, seed production were resource limited, we would expect the total average seed weight per fruit (capsule) would not continue to increase as seed number within that fruit increases, but would begin to level off and approach some upper asymptote that is less than the actual seed production could be based on the average number of ovules produced per fruit. Conversely, if seed production were pollinator limited, we would expect the average total seed weight per fruit versus seed number within a fruit to follow a linear relationship, that is each seed would add the same weight to the total as any other seed in the fruit and total seeds per fruit would only be limited by how many ovules were successfully fertilized as a result of pollinator activity. The goal of the study was to ascertain whether seed production was limited by resource allocation or pollination activity, or a combination of both, and to determine the influence of predation upon *Eds* reproduction.

MATERIALS AND METHODS

Study Area and Plant Selection

Field studies were conducted from June through September of 2000. The study area is located in the floodplain of the Santa Ana River north of Redlands, San Bernardino County, California. We selected four study sites using Burk and Jones (1990) numeric designations as a guide (Fig. 1). The climate is a mediterranean-type climate, with cool wet winters and warm dry summers (Di Castri et al. 1981). Mean temperature for the winter is 11°C and for the summer, 26°C. Mean annual precipitation is 310 mm, occurring mostly during the winter. The soil characteristic of the study sites is alluvial deposition, which consists of primary washed sands and other river deposits (Wheeler 1991).

Site One is located west of Alabama Street and immediately north of the Santa Ana River main channel, and occurs at an elevation of 360 meters. This site is considered a young succession terrace that was established during the 1969 flood (Burk and Jones 1990). Site Two is located west of Orange Street and immediately north of the Santa Ana River main stream, and occurs at an elevation of 387 meters. This site is also considered to be a young succession terrace that was established during the 1969 flood (Burk and Jones 1990). Site Three is located east of Orange Street and north of CEMEX mining company and occurs at an elevation of 396 meters. This site is considered to be an old successional terrace that was established during either the 1867 or 1862 flood (Burk and Jones 1990). Site Five is also an older successional site. It is located off the junction of Greenspot and Cone Camp Roads and occurs at an elevation of 457 meters. This site was also established either during the 1867 or 1862 flood (Burk and Jones 1990).

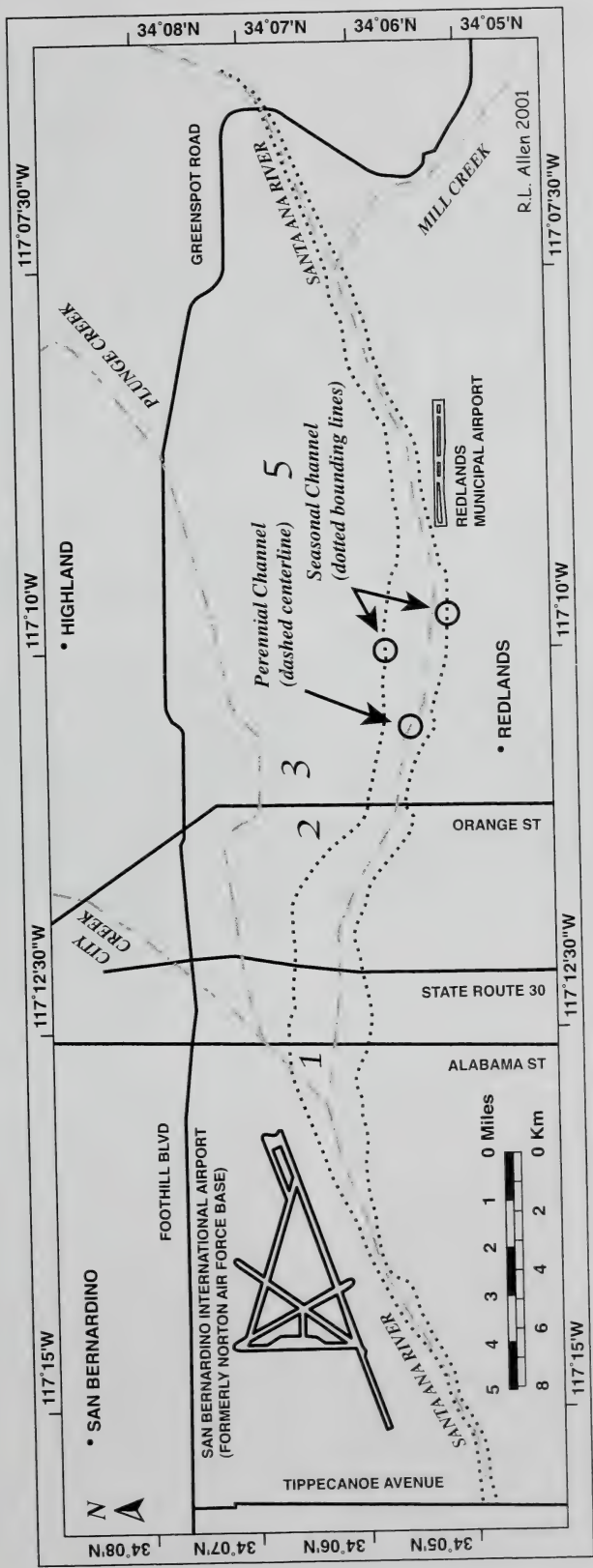On 14 and 15 June 2000, 50 healthy plants were

Fig. 1.   Location of the *Eds* Study Sites north of Redlands, San Bernardino County, California.

randomly sampled on each of the four sites for fruit collection and labelled. The plants were in the early blooming stage.

Pollinator Observations

Three pollinator observation plots were established at each of the four study sites. Each plot contained a group of about 25 healthy flowering Eds plants. These plots were located 25–30 meters from each other. Three dawn-to-dusk observations were performed (between 20 June to 6 July 2000) at each of the four study sites during the flowering season for a total of 168 hours.

Plants were observed continuously from 0600 to 2000 hours on each of the observation days. Within each hour of observation, each pollinator observation plot was observed for 10 minutes and then the observer had 10 minutes to rotate to the next plot, observe it for 10 minutes, then move on to next plot and so on throughout the entire observation day. If a floral visitor came into contact with either the stamens or stigma or both during a visit, it was considered to be a potential pollinator. Finally, the number of floral heads visited during each trip by each individual visitor was counted until the pollinator left the plot. An hourly measurement of the air temperature in the shade was recorded.

Fruit Collection and Seed Count

After the flowering season, on 6 September 2000, three floral heads with mature, but unopened fruits were collected randomly from each sampled plant at each of the four study sites. Data from 600 floral heads and 200 plants were included in the study.

Fruit set was determined for each floral head by dissecting the head and examining each flower to determine if a fruit were present. Total flower production per floral head was determined by adding fertile and infertile flowers together.

Three capsules were collected randomly from each floral head. The total number of seeds was counted for each of these capsules using a Bausch and Lomb Stereo-Zoom dissecting microscope. The mean seed number per fruit was calculated per site. Fertile and infertile seeds were determined using seed color characteristics. Brown, well-shaped seeds were assumed to be fertile, whereas other-colored or misshapen seeds were considered to be infertile as demonstrated for Eds by Phommasaysy (1999). All seeds from each capsule were stored individually in 5.7 × 8.9 cm seed envelopes.

Fruit and seed predation were determined by counting the capsules containing either developing larvae or evidence of their presence. If a larva had finished eating all seeds and left the ovary, frass was found in the hollowed fruit capsule and an exit hole was found in the ovary wall. Fruits and seeds chewed by larvae were counted and the percentage of predation on fruits was calculated from the total

number of fertile fruits for each site. Specimens of the predators, which were found in the capsules, were sent for identification to the Plant Pest Diagnostic Center of the California Department of Food and Agriculture (CDFA) in Sacramento, California.

Capsules of Eds are all about the same size regardless of how many seeds they bear. The capsules have three locules, each normally bearing five— rarely up to seven ovules (Harrison 1972), so one might expect that the normal seed set in a capsule should be around 15 if pollinator services and resources were not limiting the process. This is not what we found so, in order to determine if resources or pollinators were limiting, capsules were artificially classified into four different categories: 1 seed/capsule; 2–4 seeds/capsule; 5–7 seeds/capsule, and more than 8 seeds/capsule. These category designations were selected based on our sampling of hundreds of capsules and were our attempt to get some idea of the relative numbers of successful reproductive events, i.e., where a pollination event has resulted in a fruit being set with at least a single seed. Five samples from each category were selected.

The sampled seeds were weighed using a Mettler AE 163 Electronic Balance, which measures to a hundred-thousandths of a gram. The mean seed weight was calculated for each category for each site. These data were analyzed using a linear regression to see if there was any correlation between the number of seeds set per capsule and the weight of those seeds. Our assumption is that if there is a linear relationship between the number of seeds/capsule and total seed weight per capsule, then pollinators are limiting the number of seeds set per capsule since each new seed adds the same proportion of seed weight to the total. If on the other hand, total seed weight declines as more seeds are added to a capsule, then resources are limiting.

Statistical Analysis

Data were analyzed using a one-way analysis of variance (ANOVA) in Minitab, Version 13.2, and Poisson regression with repeated measures estimated using generalized estimating equations (GEE), Proc Genmod in SAS, Version 8.0. A Chi-square test was used to test if there were any difference in the degree of pollinator limitation among study sites. One-way analysis of variance and Tukey's pairwise comparison were used to evaluate the following variables: total flowers per head, infertile flowers per head, predation, and seed weight. Poisson regression was used to determine if there were any significant differences in the total number of seeds per capsule and fertile seeds per capsule among the study sites.

RESULTS

Primary Pollinator Observations

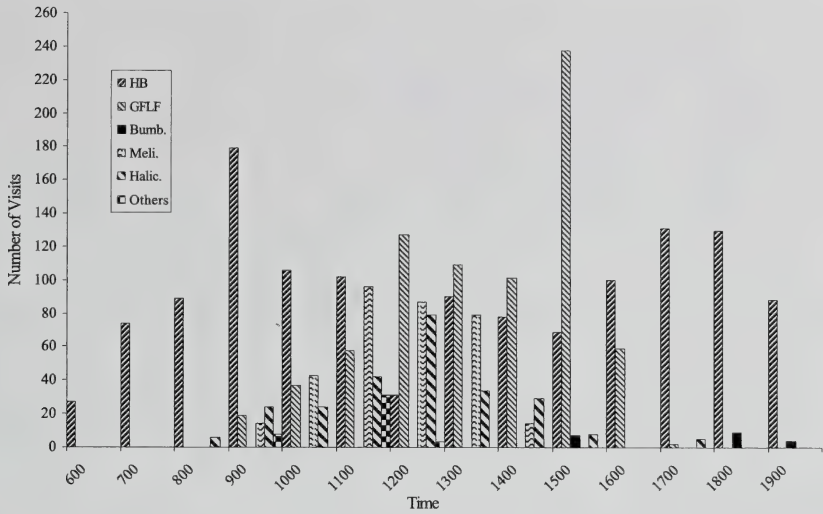The dawn-to-dusk observations performed throughout the Eds flowering season in summer

FIG. 2.   Total visits per hour observed for the major pollinators at all sites during the *Eds* flowering season of 2000. Observation periods: 20 June through 6 July. HB: hummingbirds, GFLF: Giant Flower Loving Fly, Bumb.: bumblebees, Meli.: digger bees or Melissodes spp., Halic.: halictid bees. Others include: honeybees, White-Lined Sphinx Moth, the Giant Swallowtail and Cabbage butterflies.

2000 focused on five primary pollinators or pollinator groups. The pollinators were sometimes classified together in groups for easier observation and for better data analysis and presentation. The pollinators are classified as follows 1) hummingbirds, 2) the Giant Flower Loving Fly, *Raphiomidas acton acton,* 3) the California Bumblebee, *Bombus californicus,* 4) digger bees, *Melissodes* spp., and 5) halictid bees, primarily *Halictus tripartitus* (Jones and Burk 1996). Other or secondary pollinators were: two butterflies (the Giant Swallowtail, *Papilio cresphontes,* and Cabbage White, *Pieris rapae*); the Honeybee, *Apis mellifera,* and the White-Lined Sphinx Moth, *Hyles lineata.* Throughout the surveillance period, 168 hours of observation were performed, with a total record of 2713 visits by 435 pollinators (Fig. 2).

At Site One, digger bees and halictid bees were the primary pollinators representing 40% and 20% of the total visits, respectively. These groups were followed by hummingbirds, (19%), and the Giant Flower Loving Fly (17%). This site had the lowest number of total visits, 183. It was windy during the 5 and 6 July observational periods when Site One was observed and wind could be a major contributing factor for the low pollinator activity during these days. The data suggest that digger bees favor foraging between 0900 and 1400, with peak activity at noon. The temperature during this period was between 25°C and 35°C.

The Giant Flower Loving Fly and hummingbirds dominated at Site Two with 42% and 28%, respectively, from a total of 626 visits. Halictid bees and digger bees were next at 14% and 11%. The Giant Flower Loving Fly was very active from 1100 to 1600, when the temperature was between 30°C and

36°C. Other pollinators documented at Site Two were the Giant Swallowtail, Cabbage White butterflies, and the White-Lined Sphinx moth, all accounting for 5% of the visits.

Pollinators at Site Three were more active compared to Sites One and Two with a total of 892 visits. Hummingbirds and the Giant Flower Loving Fly were the most active pollinators at 41% and 38%. Digger bees and halictid bees were next in importance at 11% and 9%. On this site, we observed the only two Bumblebees during this season. They were foraging in the early evening hours between 1800 and 1900.

Site Five had the highest total visits among the sites, 1023. Hummingbirds were the major pollinators with 72% of total visits. Hummingbirds were active throughout the daylight, but mainly in the morning and late afternoon. The hummingbirds foraged from 0600 to 1100 with a peak at 0900, and then another activity period occurred between 1300 to 1900 with a peak at 1900. The Giant Flower Loving Fly represented 13% of visits on this site, but was not as active as on Site Three. Digger bees and halictid bees were infrequent pollinators at 8% and 5%, respectively.

Fruit Collection and Seed Count

There was no significant difference among the sites in total number of flowers per floral head (one way analysis of variance, n = 600 individual floral heads, F = 0.84; df = 3, 596, P = 0.475). However, the mean number of fertile flowers per floral head showed significant differences among the sites (one way analysis of variance, n = 600 individual floral heads, F = 22.4; df = 3, 596, P < 0.0001).

TABLE 1. DESCRIPTIVE STATISTICS ON THE NUMBER OF FLOWERS PRODUCED DURING THE *Eds* FLOWERING SEASON OF 2000.

Site	Number of heads	Total flower/head		Percent of fertile flowers/head	Fertile flowers/head		Infertile flowers/head	
		Mean	SD		Mean	SD	Mean	SD
1	150	43.71	10.31	39.1	13.57	7.42	21.14	11.33
2	150	33.28	10.20	26.2	8.72	6.64	24.56	11.27
3	150	33.39	8.02	22.7	7.58	5.85	25.81	9.13
5	150	33.16	10.03	29.3	9.71	6.88	23.45	9.62

The mean number of infertile flowers per floral head also was significantly different among the sites (one way analysis of variance, n = 600 individual floral heads, F = 5.48; df = 3, 596, P = 0.001) (Table 1). The mean number of seeds per capsule (n = 1322) showed no significant differences between Site Five and Site One, but Site Two and Site Three were significantly different from Site Five (contrast from Poisson regression; P = 0.02, P = 0.001, respectively).

The mean number of fertile seeds per capsule (n = 1322) showed significant differences among Site Two, Site Three and Site Five, [(contrast from Poisson regression; P < 0.0001, P < 0.0001, P = 0.01 respectively) (Table 2)].

Pollinator versus Resource Limitation

Two different analyses were undertaken in an attempt to determine if fruit/seed set in *Eds* was being limited by pollinator or resource availability. First a Chi square test was completed to determine how fruit set was related to the published estimate of 33% as the average fruit set for self-incompatible plants like *Eds* (Sutherland 1986). The 33% level was rejected at all sites (P < 0.001). However, Sites Two, Three, and Five had less than 33%, whereas Site One had more.

A further examination of the relationship between the number of seeds produced per capsule and the total weight of those seeds was completed to determine if resources or pollinators were limiting. The data were analyzed using a curvilinear regression model. The R-squared is over 80%, and P value is <0.001. When graphed in this manner, (see Fig. 3), there is a direct relationship between these factors up to seven seeds per capsule. Beyond eight seeds per capsule this relationship begins to show a decline in total seed weight as the number of seeds per capsule increases. We assumed that this indicates that total seed weight is declining

above seven seeds per capsule because of resources being a limiting factor. We then determined the total number of capsules that had 7 or fewer seeds and the number that had eight or more seeds. The results indicate that the percentage of the capsules showing pollinator limitation among *Eds* study sites is three times greater than those where resources were the limiting factor (see Fig. 4).

Predation

The mean level of predation was significantly different among sites [(n = 600 individual floral heads, F = 59.6; df = 3, 596, P < 0.0001) (Table 3)].

DISCUSSION

Pollination is one mutualism that has the potential to control important demographic attributes of populations. Pollination by insects can be of critical importance to sexual reproduction in rare plants and most rare plant taxa rely on insect pollination and their survival often depends on the maintenance of sufficient pollinator populations (Harper 1979). Therefore, if pollinators are indeed limiting, the reproductive success of these rare plants can be negatively impacted.

Primary Pollinator Observations

This study demonstrated that the self incompatible *Eds* relies on insects and hummingbirds for most of its reproductive success. The study examined the five most prominent pollinators of *Eds*: hummingbirds, the Giant Flower Loving Fly, the California Bumblebee, Digger bees, and Halictid bees. During the study season, hummingbirds and the Giant Flower Loving Fly were the most common pollinators and had the highest number of visits overall. However, Digger and Halictid bees were more common pollinators at Sites One and Two,

TABLE 2. *Eds* SEED SET PER SITE. n = capsules examined per site.

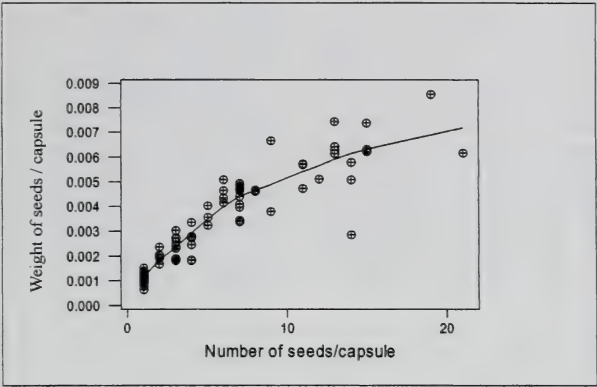| Site	n	Seeds/capsule		Fertile seeds/capsule			Infertile seeds/capsule		
		Mean	Total	Mean	Percent	Total	Mean	Percent	Total
1	358	5.2	1874	3.3	64.4	1207	1.8	35.6	667
2	364	5.6	2044	4.6	82.7	1691	0.9	17.3	353
3	375	5.9	2227	4.8	80.9	1802	1.1	19.1	425
5	227	4.7	1085	3.9	82.9	899	0.8	17.1	186

FIG. 3. Weight of seeds per capsule (mg) vs. category, with a running average superimposed (a "Loess smooth" from Minitab).

which are considered younger sites. Hummingbirds and the Giant Flower Loving Fly were the major pollinators at the older sites, Three and Five, thus confirming differences in pollinator combinations with site age. It appears from these data that the predominate pollinators at each of the sites may be the ones that are nesting in the vicinity of the plants at those sites. Further study of the sites needs to be done to determine if the predominate pollinators do, in fact, nest in the areas where they are the most common visitors at *Eds* flowers.

Site One had the least pollinator visitations among the sites, and was the only one that exceeded the 33% fertility (fruit set) rate taken from Sutherland (1986) for self incompatible plants. One possible reason for this could have been adverse weather conditions that occurred during the dawn to dusk observations done at this site, since microclimate may operate as a constraint at many points in the chain of processes necessary for a successful pollination/fertilization event. In addition, observations show that insect activity was related strongly to weather conditions at the different sites since the dawn to dusk observations at the sites were not

all done simultaneously. Insect visitation rates dropped when the wind velocity was above 25 km/hr (this wind speed was exceeded during our observations at Site One, but not at the other sites) and/or the temperature was above 40°C or below 20°C. Generally, pollinator activity was greater between 1000 and 1600 hours, with bees preferring morning hours and the Giant Flower Loving Fly, the afternoon. Hummingbirds were active in both the early morning and late afternoon hours, and seemed much less affected by weather conditions than insects. During this study, the California Bumblebee was observed only once at Site Three in the late afternoon. Further studies of pollinator life histories, habitat requirements, and ecological interactions may help to explain pollinator distributions in the study area. This information is important in elucidating the dynamics of the pollination biology of *Eds*.

Pollinator-Resource Limitation

Reproductive success of *Eds* appears to be pollinator and resource-limited, and also affected by predation. However, the pattern was not consistent among the study sites, nor is the degree similar for all components of reproduction examined. Mean fertilization success, i.e., natural fruit set, was lower than 33% for Sites Two, Three, and Five, but higher for Site One. Insufficient pollination (determined to occur in 75% of the fruits examined where the
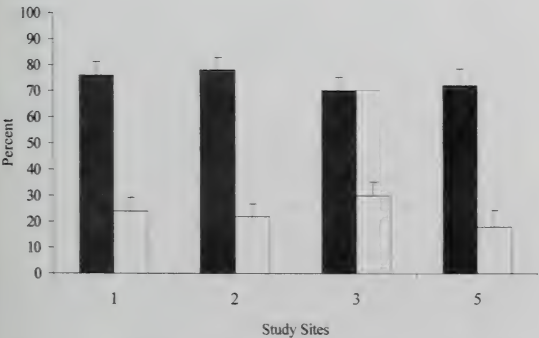

FIG. 4. Percentage of pollinator limitation (black bars), resource limitation (white bars) among the study sites (mean + 1 SE).

TABLE 3. THE DEGREE OF PREDATION ON *EDS* CAPSULES, BASED ON TOTAL NUMBER OF FRUITS PER SITE.

Site	Number of heads with predation	Fertile flowers/site	Fruits eaten by larvae	Percent of predation
1	69	2036	746	36.6
2	48	1309	158	12.1
3	23	1137	33	2.9
5	125	1457	910	62.5

number of seeds per fruit were seven or fewer) limited the number of fruits matured per plant and appears to have limited the number of seeds initiated per fruit. Fruit production in *Eds* appears to be limited by infrequent pollinator visits at three of the four study sites. The amount of pollen transferred may also limit fruit/seed production. Even with optimum high quality pollination, *Eds* may not be able to develop all of the fruits because of resource-limitation (determined to occur in 25% of the fruits), which may cause abortion of developing ovaries or ovules (Stephenson 1981).

The average natural seed set for all study sites was 5.3 seeds per capsule, which is substantially below the potential seed set per fruit in the normal flower of 15 (rarely to 21 when each of the three locules in the fruit has seven ovules rather than the normal five). Since this number is well below seven, or the number of seeds per fruit in which the only limitation to seed production seems to be pollinator activity, the major limiting factor to fruit and seed production in *Eds* seems to be pollinator availability. Further, the number of ovules fertilized and the number matured can be shown as a fraction of the number of ovules available (Table 2), and the abortion rate can be calculated as the difference between the percentage of ovules fertilized and the percentage matured (Schemske et al. 1978).

In this study, *Eds* plants initiated more flowers than fruits (Table 1), a pattern common to most plant species (Stephenson 1981). More *Eds* flowers set fruit when hand-pollinated than when naturally pollinated, and pollen and pollinator services were considered to be limiting factors in fruit production in 1990 (Munoz 1991). Resource-limitation is an additional factor for aborted fruits and in cases where the number of seeds per fruit exceeded seven, as lack of available resources limits fruit and seed production as well as effects pollen production and quality.

Seed Predation

Seed predation is different among the study sites, reaching 62.5% at Site Five. The rate of predation in the 2000 *Eds* flowering season for each site was: 1) 36.6%, 2) 12.1%, 3) 2.9%, and 5) 62.5%. Clearly, high predation percentages, as in Sites One and Five, can have a selective influence on *Eds* populations. Predation can affect plant resource allocation in that, when predators damage plant tissue, rates and/or amounts of resources translocated to various parts of the plant are modified. Removal or destruction of flowers and immature fruits can change the balance between vegetative growth and reproduction and can also increase the number of flowers and fruits produced later in the season. Removal of reproductive tissues can alter the longevity of the life span of individual plants (Hendrix and Trap 1981). When insects destroy the pericarp of a fruit, fruit abortion can occur (Stephenson

1981). Sometimes, insects transmit diseases or leave scars where diseases can enter. The saliva of some insects can also cause fruit abortion.

Eds on Sites One and Five have the highest fertility rates, 39.1% and 29.3%, and the highest predation rates, 36% and 62.5%, respectively. This suggests that large seed yields are the result of more obvious flowers that attract more pollinators and produce more fruits/seeds that, in turn attract more predators than smaller yields. In this study, there is a positive correlation between successful pollinator activities and the degree of predation. This could mean that pollinators and predators react in similar ways to the same plant populations. Thus, whatever makes an individual *Eds* plant attractive to pollinators seems to also make it attractive to fruit/seed predators. Our study seems to show a positive correlation between the level of predation and plant fecundity, suggesting that, at least during the 2000 flowering season, competition for pollinators was high enough to allow those plants on Sites One and Five to have the highest relative fecundity. The activities of pollinators and predators are accountable, in part, for the observed fruit and seed set of *Eds*.

Summary

This study explores some of the factors that may affect the reproductive biology of *Eds*. *Eds* is a rare, self-incompatible, perennial that relies on insects and hummingbirds for its reproductive success. During the 2000 flowering season, hummingbirds and the Giant Flower Loving Fly were the most common pollinators, and had the highest number of visits overall, especially on Sites Three and Five. However, Digger and Halictid Bees were more common pollinators at Sites One and Two. This study suggests that reproductive success of *Eds* is pollinator and resource-limited, and is also affected by high predation rate. Mean fertilization, i.e., natural fruit set, was lower than 33% for Sites Two, Three, and Five, but higher for Site One. Differences in the limits of seed/fruit production for *Eds* seem to be related to the variation among populations in pollinator visitation rates and predation. Resource availability has also limited seed production, but to a lesser extent. However, if severe enough, it could, in theory, produce differences in population dynamics. Results indicate that pollinator availability limits seed production per capsule until seven seeds are produced and, above that level, seed production per capsule is resource limited. Evidence shows that predators of *Eds* significantly reduce the number of seeds set on the successfully pollinated flowers. The effects of predators on *Eds* emphasizes the importance of knowing about the timing of predator life history stages in relation to the development of their prey resources. A demographic study of *Eds* could incorporate these factors and determine how they may affect the long-term success of this rare plant species.

Rare plants are often indicators of the overall health of the ecosystem in which they occur. Since most flowering plants, including *Eds*, must have an external vector to facilitate their reproduction, a thorough knowledge of the reproductive biology of rare plants like *Eds*, including a knowledge of their seed predators, is often critical to our ability to understand the basic requirements for their survival and to create management plans to maintain the health of the ecosystems in which they occur. The health of the pollinating organisms must also be maintained if the rare species is to survive.

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INSECTS ON *PHOLISMA SONORAE* (LENNOACEAE) FLOWERS AND THEIR CONSPECIFIC POLLEN LOADS

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Abstract

Insects collected on *Pholisma sonorae* (A. Gray) Yatskievych flowers in the Algodones Dunes, Imperial County, California, were identified and their pollen loads extracted and categorized as *P. sonorae* or non-*P. sonorae*. Flowers were present during 3 April to 12 June 2001, most abundant on 16 May 2001, and open during the day. *Bembix rugosa* J. Parker (Hymenoptera: Sphecidae) was collected during most of the flowering season and carried most *P. sonorae* pollen but had a low flower constancy (percent *P. sonorae* pollen). *Leptoconops californiensis* Wirth and Atchley (Diptera: Ceratopogonidae) was collected early in the flowering season when other insects were absent and had a high flower constancy. *Aphoebantus* sp. near *rattus* Osten Sacken, *Aphoebantus marcidus* Coquillett, and *Aphoebantus mus* Osten Sacken (Diptera: Bombyliidae) were the most-collected insects late in the flowering season and carried low to moderate amounts of *P. sonorae* pollen. One *Toxomerus marginatus* (Say) (Diptera: Syrphidae), *Toxophora pellucida* Coquillett (Diptera: Bombyliidae), *Mythicomyia intermedia* Melander, *Mythicomyia spectabilis* Hall and Evenhuis, and *Mythicomyia uncata* Melander (Diptera: Mythicomyiidae) also was collected. Conserving *P. sonorae* may require conserving *B. rugosa, L. californiensis,* and *Aphoebantus* spp. as pollinators.

Key Words: Lennoaceae, *Pholisma sonorae*, Insecta, pollen load, flower constancy.

Sand food, *Pholisma sonorae* (A. Gray) Yatskievych, is a plant inhabitant of sand dunes that ranges from the Salton Sea in southern California southeast through southwestern Arizona to the northern edge of the Gulf of California, Sonora, Mexico (Nabhan 1980). *Pholisma sonorae* is a plant parasite that attaches to the roots of dune perennials, mostly shrubs (Armstrong 1980a; Nabhan 1980), and produces a prostrate, mushroom-shaped inflorescence atop a succulent, buried stem (Kuijt 1969; Armstrong 1980a, b; Yatskievich 1985). Inflorescences of *P. sonorae* are 3 to 10 cm in diameter (Munz 1974), annual, and woolly due to long hairs produced by sepals (Kuijt 1969). Flowering by *P. sonorae* is centrifugal (Armstrong 1980a). Corollas are purple, tubular, and approximately 8 mm long (Munz 1974). The floral entrance encloses a ring of anthers, arising high on the corolla tube, encircling a central and slightly-lower stigma (Kuijt 1969).

The rarity of *P. sonorae* throughout its range (Yatskievych 1993) has caused interest in conserving populations of the plant (Nabhan 1980). Conserving plants cross-pollinated by animals requires conserving their pollinators. Yatskievych (1985) hypothesized *P. sonorae* is pollinated by insects due to its small tubular corolla, floral nectar, and extremely-low seed set as evidenced from old inflorescences. Flowers of *Pholisma culiacana* (Dressler and Kuijt) Yatskievych in Mexico were visited by flies, beetles, and small butterflies (Dressler and Kuijt 1968). Insect species visiting *P. sonorae* flowers are unknown. This study determines these insect species and compares their *P.*

sonorae pollen loads and estimated flower constancies.

Methods

The study area was located (32°42′50″N, 114°55′4″W) at an elevation of 60 m in the Algodones Dunes, Imperial County, California, 19 km west of the Arizona State line and 1 km north of the International Boundary with Mexico. Habitat within the study area was sparsely vegetated sand dunes protected from vehicles. Dominant vegetation included the perennials *Eriogonum deserticola* S. Watson (Polygonaceae) and *Tiquilia plicata* (Torrey) A. Richardson (Boraginaceae) and the annual *Abronia villosa* S. Watson (Nyctaginaceae). Climate at Yuma, Arizona, (30 km east) is summarized as average maximum and minimum temperatures of 42.7°C and 26.9°C during July and 20.4°C and 6.8°C during January and an average yearly total rainfall of 74 mm occurring mostly during August to October (27 mm) and December to March (32 mm) (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Reno, Nevada).

Pholisma sonorae flowers were observed at three sites approximately 0.1 km apart along a west to east transect within the study area. The west site was partly under the canopy of an *E. deserticola* shrub and contained 2 to 12 *P. sonorae* inflorescences within a 1 m² area. The middle site was <5 m from a *T. plicata* shrub and contained 3 to 21 *P. sonorae* inflorescences within a 12 m² area. The east site was 3 to 4 m from an *E. deserticola* shrub

and contained 5 to 17 *P. sonorae* inflorescences within a 3 m² area.

Phenologies of *P. sonorae* flowering were determined. Seasonal phenology was determined by counting inflorescences and flowers with open or closed corollas in the morning weekly during 3 April to 12 June 2001. Diurnal phenology was examined on 25 April 2001. I counted flowers every 1.5 hr during 0630 to 1900 Pacific Daylight Time (PDT) in each of four stage-classes: (1) corolla completely closed, (2) corolla partly open with opposite petals touching, (3) corolla open but ovoid, (4) corolla completely open and circular. Flower abundances were plotted against observation times averaged across sites within each 1.5 hr period.

Pholisma sonorae flowers were examined for insects 1 to 3 d per week during 3 April to 12 June 2001. I examined flowers for a total of 123 hr during 0600 to 2000 PDT with most (109 hr) examinations during 0700 to 1400 PDT. Sites were observed (34 [10–95] min) in rotation during each day. I measured air temperature (±1°C) with a digital thermohygrometer (Protimeter, Woburn, Massachusetts) approximately 10 cm above the sand at the beginning of each site's observation period.

Insects on *P. sonorae* flowers were collected. I collected Ceratopogonidae by inverting a 1-dram screw-cap vial over the flower, righting the vial after the insect flew upwards into it, and filling the vial with 70% ethanol. Larger Diptera and Hymenoptera were collected with a 2-dram screw-cap vial pressed onto the spout of a 19-cm diameter plastic funnel. The funnel was inverted over the entire inflorescence and righted after the insect flew upwards into the vial. I then washed the inside of the funnel with 70% ethanol until the vial was filled. Insects dying before flying into the vial were collected with forceps washed with ethanol. I saw butterflies on *P. sonorae* inflorescences but was unable to approach and collect them. Instead, different butterflies resembling the same species were collected by net.

Pollen was extracted from insects collected on *P. sonorae* flowers by shaking each vial for 1 min with a vortex shaker and centrifuging the ethanol for 10 min at 3K rpm. The centrifuged residue was suspended in water (5 ml) and poured into an evaporating dish with a 4 cm diameter flat bottom. Polyvinyl alcohol (1.5 ml of 12.5% solution, Dafni 1992) was stirred into the residue suspension, dried 2 hr at 50°C, and peeled from the dish.

Polyvinyl-alcohol films were compressed between microscope slides and examined at 100× with transmitted light. I counted and categorized all pollen grains as *P. sonorae* or non-*P. sonorae*. *Pholisma sonorae* pollen was recognized by its 2-layered margin (distinct nexine and sexine) and 3-colporate shape in polar view (Drugg 1962; Yatskievych and Zavada 1984). I determined these characters by comparing pollen grains collected from *P. sonorae* with pollen grains collected from

other plant species at the study area and preserved and fixed as above. *Pholisma arenarium* Hook., the only other Lennoaceae species in California (Yatskievych 1993), produces pollen grains also with distinct nexine and sexine but typically with a 4-colporate shape (Drugg 1962; Yatskievych and Zavada 1984). *Pholisma arenarium* did not occur in the study area and 4-colporate pollen grains were not observed in the films.

Collected insects were identified, and voucher specimens were deposited at the California Academy of Sciences, San Francisco (Sphecidae), Bishop Museum, Honolulu, Hawaii (Bombyliidae and Mythicomyiidae), US National Museum, Washington, D.C. (Syrphidae and Ceratopogonidae), Canadian National Collection, Ottawa, Canada (Ceratopogonidae), and Natural History Museum of Los Angeles County, California (Nymphalidae).

Pollen loads from insects collected on flowers were analyzed by first summing frequencies of *P. sonorae* pollen grains and frequencies of non-*P. sonorae* pollen grains across specimens within insect species. *Mythicomyia* spp. were combined due to low sample sizes. Frequencies of *P. sonorae* pollen grains from species were compared (χ^2) with those expected if each insect specimen carried the same amount of *P. sonorae* pollen. The overall analysis then was partitioned into independent χ^2 comparisons (Agresti 1990): (1) between Hymenoptera and Diptera, (2) between Diptera suborders Nematocera and Brachycera, (3) between Syrphidae and other Brachycera (Mythicomyiidae and Bombyliidae), (4) between Mythicomyiidae and Bombyliidae, (5) between Bombyliidae genera *Toxophora* and *Aphoebantus,* and (6) among *Aphoebantus* spp. Flower constancies, estimated as ratios of *P. sonorae* pollen to non-*P. sonorae* pollen (Dafni 1992), were compared (χ^2) among insect species. The overall analysis again was partitioned into the above χ^2 comparisons. Flower constancies were presented as percentages of pollen grains categorized as *P. sonorae*.

RESULTS

Numbers of *P. sonorae* flowers and inflorescences at the study sites increased during April and early May 2001, reached a maximum of 1294 flowers on 43 inflorescences on 16 May 2001, and decreased during late May and June 2001 (Fig. 1). *Pholisma sonorae* flowers opened during the day (Fig. 2). Numbers of flowers with partly-open corollas decreased during the morning and increased slightly during the afternoon. Open flowers with ovoid corollas were observed during 0630 to 1900 PDT. Completely-open flowers with circular corollas were present during 0800 to 1600 PDT and peaked in abundance at 1300 PDT.

Ten insect species in two orders and five families were collected on *P. sonorae* flowers (Table 1, Fig. 3). I collected *Bembix rugosa* J. Parker (Hymenop-
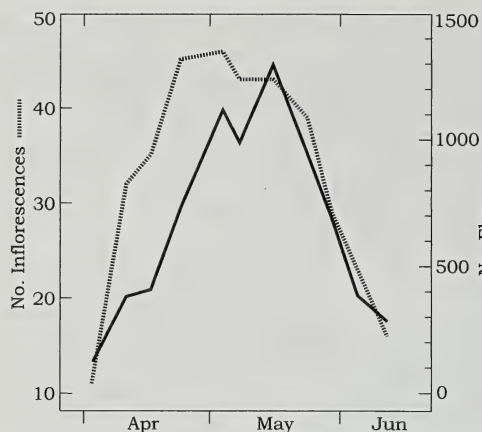
FIG. 1. Abundances of *Pholisma sonorae* inflorescences and flowers at three plant-aggregations during 2001.

tera: Sphecidae), *Leptoconops californiensis* Wirth and Atchley (Diptera: Ceratopogonidae), *Toxophora pellucida* Coquillett (Diptera: Bombyliidae), *Aphoebantus* sp. near *rattus* Osten Sacken, *Aphoebantus marcidus* Coquillett, and *Aphoebantus mus* Osten Sacken (Diptera: Bombyliidae), *Mythicomyia intermedia* Melander, *Mythicomyia spectabilis* Hall and Evenhuis, and *Mythicomyia uncata* Melander (Diptera: Mythicomyiidae), and *Toxomerus marginatus* (Say) (Diptera: Syrphidae). *Bembix rugosa* (4 males and 7 females) was collected throughout most (25 April to 6 June 2001) of the sampling period (Fig. 3). *Leptoconops californiensis* (8 males and 8 females) was collected during early spring (18 April to 4 May 2001) when air temperatures (28°C to 39°C) were lower, whereas *Aphoebantus* spp. were collected during late spring (17 May to 4 June 2001) when air temperatures (42°C to 46°C) were higher (Fig. 3). *Bembix rugosa, L. californiensis,* and *Aphoebantus* spp. were collected at all three sites.

Collected butterflies (n = 9) resembling those seen at *P. sonorae* inflorescences were identified as *Vanessa cardui* (Linnaeus) (Lepidoptera: Nymphalidae). Butterflies assumed to be *V. cardui* were observed at *P. sonorae* inflorescences 14 times during 24 April to 4 May 2001.

Pholisma sonorae pollen was extracted from nine of the 10 insect species collected on *P. sonorae* flowers (Table 1). Frequencies of *P. sonorae* pollen grains from insects differed among species ($\chi^2 = 7056$, df = 7, P < 0.001). Frequencies of *P. sonorae* pollen grains differed between Hymenoptera and Diptera ($\chi^2 = 7054$, df = 1, P < 0.001) with *B. rugosa* carrying 92.1% of *P. sonorae* pollen grains extracted. Frequencies of *P. sonorae* pollen grains also differed among species of *Aphoebantus* ($\chi^2 = 49.6$, df = 2, P < 0.001). Frequencies of *P. sonorae* pollen grains did not differ between Diptera suborders Nematocera (*L. californiensis*) and Brachycera ($\chi^2 = 0.85$, df = 1, P = 0.36), between

Syrphidae and other Brachycera ($\chi^2 = 2.08$, df = 1, P = 0.15), between Brachycera families Mythicomyiidae and Bombyliidae ($\chi^2 = 0.40$, df = 1, P = 0.53), or between Bombyliidae genera *Toxophora* and *Aphoebantus* ($\chi^2 = 3.49$, df = 1, P = 0.062).

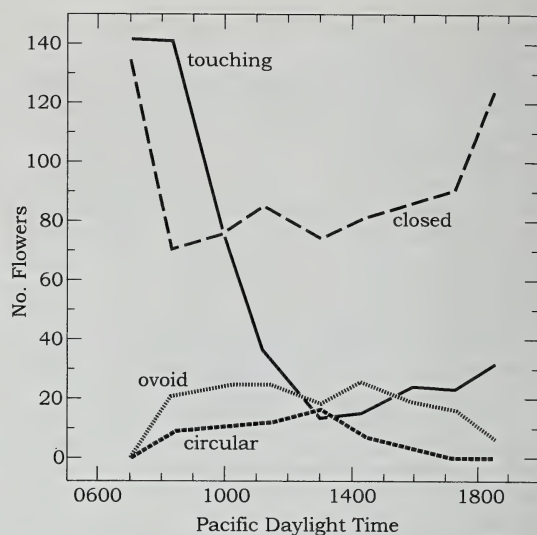Flower constancies for *P. sonorae* differed ($\chi^2 =$

FIG. 2. Flowering by *Pholisma sonorae* at three plant-aggregations on 25 April 2001. Corollas categorized as closed, partly open with opposite petals touching, open but ovoid, or completely open and circular.
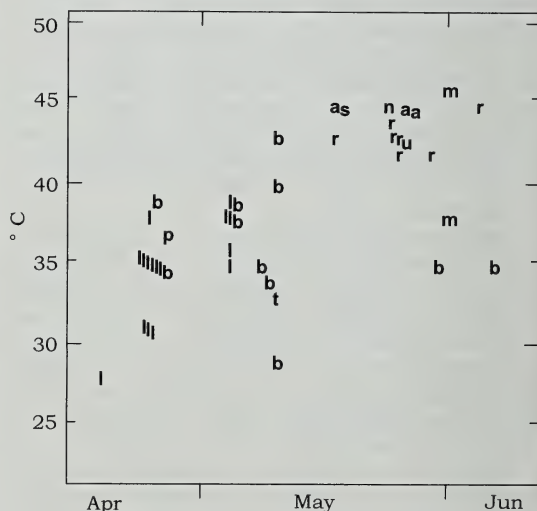

FIG. 3. Air temperatures versus dates when insects were collected from *Pholisma sonorae* flowers during 2001. Species plotted as b = *Bembix rugosa*, l = *Leptoconops californiensis*, r = *Aphoebantus* sp. near *rattus*, a = *Aphoebantus marcidus*, m = *Aphoebantus mus*, p = *Toxophora pellucida*, n = *Mythicomyia intermedia*, s = *Mythicomyia spectabilis*, u = *Mythicomyia uncata*, t = *Toxomerus marginatus*. Overlying symbols diagonally offset.

TABLE 1. NUMBER OF SPECIMENS OF INSECT SPECIES COLLECTED ON *PHOLISMA SONORAE* FLOWERS AND MEAN AND RANGE OF NUMBER OF *P. SONORAE* POLLEN GRAINS, AND PERCENT *P. SONORAE* POLLEN, EXTRACTED FROM SPECIES. [a] Weighted by no. pollen grains. [b] No. specimens with pollen = 11. [c] No. specimens with pollen = 6. [d] Specimen without pollen.

Species	n	*P. sonorae* pollen grains		% *P. sonorae* pollen	
		Mean	Range	Mean[a]	Range
Bembix rugosa	11	246	44–707	37.1	6–96
Leptoconops californiensis	16	7.4	0–51	85.6[b]	0–100[b]
Aphoebantus sp. near *rattus*	7	3.1	0–16	47.8[c]	0–100[c]
Aphoebantus marcidus	3	16	2–30	63.2	25–73
Aphoebantus mus	2	7.0	4–10	73.7	71–80
Toxophora pellucida	1	2.0	—	33.3	—
Mythicomyia intermedia	1	0.0	—	—[d]	—[d]
Mythicomyia spectabilis	1	19	—	100	—
Mythicomyia uncata	1	4	—	50.0	—
Toxomerus marginatus	1	3.0	—	60.0	—

193.8, df = 7, P < 0.001) among insect species (Table 1). Flower constancies differed between Hymenoptera and Diptera (χ^2 = 162.9, df = 1, P < 0.001) with Diptera showing greater flower constancy. Flower constancies differed between Diptera suborders Nematocera and Brachycera (χ^2 = 20.9, df = 1, P < 0.001) with greater flower constancy exhibited by the nematoceran *L. californiensis*. Flower constancies also differed between Brachycera families Mythicomyiidae and Bombyliidae (χ^2 = 6.94, df = 1, P = 0.008) with Bombyliidae showing less flower constancy. Flower constancies did not differ between Syrphidae and other Brachycera (χ^2 = 0.015, df = 1, P = 0.90), between Bombyliidae genera *Toxophora* and *Aphoebantus* (χ^2 = 1.63, df = 1, P = 0.20), or among *Aphoebantus* spp. (χ^2 = 4.61, df = 2, P = 0.10).

DISCUSSION

Diurnal insects are most likely to pollinate *P. sonorae* due to the species' daytime flowering. Insects with greatest potential for pollinating *P. sonorae* in order of likely importance are *B. rugosa*, *L. californiensis*, and *Aphoebantus* spp. *Bembix rugosa* carried the most *P. sonorae* pollen and was collected throughout most of the flowering season. *Leptoconops californiensis* had a high flower constancy and was collected early during the flowering season when other insects were absent. *Aphoebantus* spp. were the most-collected insects late during the flowering season and had low to moderate *P. sonorae* pollen loads and moderate flower constancies. Thus *B. rugosa*, *L. californiensis*, and *Aphoebantus* spp. may need to be conserved to ensure *P. sonorae* pollination throughout its flowering. *Pholisma sonorae* may depend on additional pollinator species, such as *V. cardui* or insects in other areas of the plant's range.

Pholisma sonorae pollen loads and flower constancies were related to insect size. High *P. sonorae* pollen load and low flower constancy were measured on the largest insect, *B. rugosa*. *Bembix rugosa*'s unusually-long labrum (Bohart and Horning

1971) may have contributed to its ability to carry copious *P. sonorae* pollen. This wasp commonly was observed standing on the inflorescence and probing flowers with its proboscis. Low *P. sonorae* pollen load and high flower constancy were measured on the smallest insect, *L. californiensis*. *Leptoconops californiensis* was the only species I saw walking into the floral entrance. The inverse relationship between flower constancy and insect size suggests larger insects were stronger fliers and more able to visit flowers of a variety of plant species. Indeed, I observed *B. rugosa* rapidly flying to *P. sonorae* aggregations from distances > 30 m, whereas *L. californiensis* was seen approaching and departing flowers while hovering < 1 m from the same inflorescence. I also watched *L. californiensis* fly to flowers from the same direction in a slow, zigzag pattern, suggesting the species was attracted by floral odors (Wiesenborn and Baker 1990).

Strategies for conserving *B. rugosa*, *L. californiensis*, and *Aphoebantus* spp. would be improved by understanding their life requirements. *Bembix rugosa* is a relatively-rare desert wasp ranging from northwest Nevada and southwest Utah south through Arizona and southern California into Baja California (Evans and Matthews 1968). *Bembix* wasps generally nest in groups by digging a burrow in sand or sandy soil and continually provisioning it with flies captured to feed larval offspring (Bohart and Horning 1971). *Bembix rugosa* in Baja California Sur dug burrows approximately 1 m long and 20 to 40 cm deep in sand dunes stabilized by plants and provisioned them with muscoid Diptera, Syrphidae, Bombyliidae, Therevidae, Asilidae, and Mydidae (Evans 1976). Nests dug into sand dunes by *Bembix inyoensis* Kimsey and Kimsey at Death Valley, California, were provisioned primarily with locally-common *Aphoebantus* spp. (Kimsey et al. 1981). *Leptoconops californiensis* inhabits areas with sandy soil in the deserts of southern California and Sonora, Mexico (Mullens et al. 1997). Nothing is known of its biology except for the recent discovery of blood-feeding by adult females on five

species of lizards (Mullens et al. 1997). Ceratopogonidae females consume vertebrate or invertebrate blood for egg maturation, and both sexes may visit flowers (Downes and Wirth 1981). Ceratopogonids in the genus *Forcipomyia* are important pollinators of cocoa in the tropics (Wirth 1991). *Leptoconops* larvae usually develop in moist sand frequently containing organic material (Wirth and Atchley 1973). Larvae of *Leptoconops torrens* Townsend in a southern California desert canyon were found in sand that was moist and supporting algae (Brenner and Wargo 1984). Bombyliidae are pollinators of a diverse array of plant species, especially those producing blue, violet, or purple flowers (Kastinger and Weber 2001). The requirements of larval bombyliids are not well known, but the few species studied are parasites of a wide range of insect larvae or pupae or predators of grasshopper eggs (Hall 1981).

The dependence of *P. sonorae* on cross-pollination remains to be estimated to determine the plant's reliance on pollinators, including *B. rugosa, L. californiensis,* and *Aphoebantus* spp. The sparse knowledge and likely-dissimilar life requirements of these insect species preclude recommending specific strategies for their conservation. For example, sandy soils with subtle differences in texture and moisture may be needed by *B. rugosa* for burrowing and by *L. californiensis* for larval development. Prey or host insects are required by *B. rugosa* and *Aphoebantus* spp., and the former may eat the latter. The lizards that *L. californiensis* need for a source of blood also depend on insects for food. Perpetuating *P. sonorae* likely requires conserving not only its host plants, but a collection of other dune plants diverse and abundant enough to support a sufficient community of insects.

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NEW DISTRIBUTIONS AND HOSTS FOR MISTLETOES PARASITIZING PINES IN SOUTHERN MEXICO AND CENTRAL AMERICA

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Abstract

New information on the distribution and host range of several mistletoes that commonly parasitize pines (*Pinus* spp., Pinaceae) in southern Mexico and northern Central America is summarized from field observations and specimen collections made from 1997–2002. The discovery of a disjunct population of *Arceuthobium hawksworthii* in Honduras nearly 350 km from the Mountain Pine Ridge of Belize indicates it is probably more widespread than previously believed. In Chiapas, Mexico, *A. hondurense* does not parasitize *Pinus pseudostrobus,* even when this pine is growing close to severely infected *P. tecunumanii.* We found that *P. oocarpa* is not a principal host of *A. aureum* subsp. *aureum* in Guatemala. We are the first to report *A. aureum* subsp. *petersonii* on *P. maximinoi.* Additional populations of *A. guatemalense* were discovered in western Guatemala and southwestern Chiapas, Mexico. We report *A. globosum* subsp. *grandicaule* in Chiapas on *P. pseudostrobus.* We have observed *Psittacanthus angustifolius* on *P. oocarpa* in northwestern El Salvador but have not yet observed *Psittacanthus schiedeanus* on pines in Central America or southern Mexico. *Struthanthus deppeanus* is uncommon in Honduras and Guatemala but is common in central Chiapas, Mexico where it parasitizes several pine species.

Key Words: *Arceuthobium, Psittacanthus, Struthanthus, Pinus.*

Introduction

Mistletoes in the genera *Arceuthobium* (Viscaceae), *Psittacanthus,* and *Struthanthus* (Loranthaceace) have been reported parasitizing pines (*Pinus* spp., Pinaceae) in southern Mexico or Central America (Scharpf et al. 1997; Geils and Vazquez Collazo 2002). Dwarf mistletoes (*Arceuthobium* spp.) are well known parasites of pines in these regions causing increased mortality and reduced

growth of severely infected trees (Hawksworth and Wiens 1996; Hawksworth et al. 2002). All of the dwarf mistletoes in southern Mexico and Central America are parasites of pines and Hawksworth and Wiens (1972, 1996) provide detailed discussions of the evolution of dwarf mistletoes and their pine hosts. Mistletoes in the genus *Psittacanthus* also parasitize pines in many areas of Mexico and Central America (Kuijt 1987; Vazquez Collazo 1993, 1994; Scharpf et al. 1997; Vazquez Collazo and
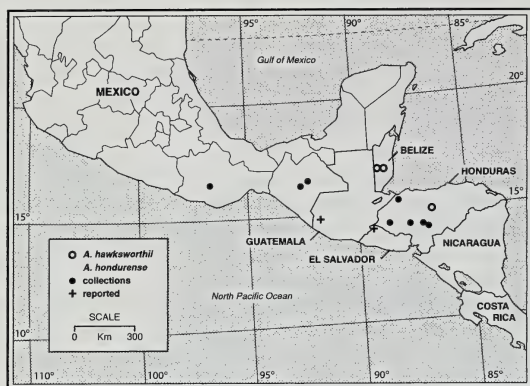
Geils 2002). A few species of *Struthanthus* also parasitize pines in Central America and southern Mexico (Kuijt 1975; Scharpf et al. 1997; Geils and Vazquez Collazo 2002). Except for Hawkworth and Wiens (1996), these reports and most herbarium specimens frequently do not include information on which species of pines are parasitized by these mistletoes. Therefore, we summarize below reported pine hosts for the mistletoes commonly found on pines in southern Mexico and Central America and report new hosts and/or distributions for these mistletoes in Honduras and Guatemala, Central America and in Chiapas and Oaxaca, Mexico. Our classification of pine hosts is based on Farjon and Styles (1997). Specimens of these mistletoes on the new hosts reported here have been deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff and/or the Herbario, Escuela Nacional de Ciencias Forestales, Siguatepeque, Honduras.

VISCACEAE

Arceuthobium hawksworthii Wiens & C. G. Shaw III

Arceuthobium hawksworthii is a rare species primarily distributed in the Mountain Pine Ridge area of western Belize (Wiens and Shaw 1994; Hawksworth and Wiens 1996; Mathiasen et al. 1998). It has recently been found in north-central Honduras (Mathiasen et al. 2002a) (Fig. 1).

The principal host of *Arceuthobium hawksworthii* is Caribbean pine (*Pinus caribaea* Morelet var. *hondurensis* (Senecl.) Barr.) (Table 1). It is also known on *Pinus tecunumanii* Eguiluz & J. P. Perry (which some authors treat as *Pinus oocarpa* Schiede ex Schlecht. var. *ochoterenai* Martinez, Perry 1991) in Belize. However, this pine has been tentatively classified as a secondary host (Mathiasen et al. 1998).

The discovery of a disjunct population of *Arceuthobium hawksworthii* in Honduras nearly 350 km from the Mountain Pine Ridge of Belize indicates it is probably more widespread than previously believed. This dwarf mistletoe has a lower elevation limit of approximately 500 m and it occurs as high as 980 m in Belize. The reasons for its lower elevation limit are unknown as its host is widely distributed in Belize below 500 m (Wiens and Shaw 1994). Our attempts to locate this dwarf mistletoe in Guatemala have been unsuccessful (Mathiasen et al. 1998), but it is probable that *Arceuthobium hawksworthii* occurs there and at additional locations in Honduras.

Arceuthobium hondurense Hawksw. & Wiens

Hawksworth and Wiens (1996) suggested that *Arceuthobium hondurense* was extremely rare and may be on the verge of extinction because of extensive harvesting of pines throughout Honduras. However, this dwarf mistletoe has now been discovered at additional locations in Honduras and in Mexico (Beatty et al. 1998; Mathiasen et al. 2001, 2002b) (Fig. 1). Its discovery in Mexico indicates that its distribution is far more widespread than previously believed (Hawksworth and Wiens 1996). It occurs in Guatemala and possibly El Salvador because earlier reports of a "black" dwarf mistletoe from Guatemala and a dwarf mistletoe in El Salvador are most probably *Arceuthobium hondurense* (Hawksworth and Wiens 1972, 1977, 1996). However, our attempts to find this dwarf mistletoe in Guatemala based on these reports (Department San Marcos) and in El Salvador (Monte Cristo National Park) have not been successful.

The principal hosts of *Arceuthobium hondurense* are *Pinus oocarpa* Schiede ex Schlecht. and *Pinus tecunumanii* in Honduras and *Pinus tecunumanii* in Chiapas and Oaxaca, Mexico (Table 1). *Arceuthobium hondurense* has been reported on *Pinus maximinoi* H. E. Moore from Cusuco National Park, Honduras (Hawksworth and Wiens 1996). However, we have not observed infection on this pine when it was growing near severely infected *Pinus tecunumanii* in Cusuco or Celaque National Parks, Honduras (Mathiasen et al. 2000a). Therefore, we believe the report of this dwarf mistletoe on *Pinus maximinoi* was based on misidentification of the host in Cusuco National Park (Mathiasen et al. 1998). In Chiapas, Mexico this dwarf mistletoe does not parasitize *Pinus pseudostrobus* Lindl., even when this pine is growing close to severely infected *P. tecunumanii*. Therefore, we have listed this pine as immune to *Arceuthobium hondurense* (Table 1).

Arceuthobium aureum subsp. *aureum* Hawksw. & Wiens

Arceuthobium aureum subsp. *aureum* occurs in the low elevation pine forests of central Guatemala,

TABLE 1. MISTLETOE HOST RANGE BASED ON NATURAL SUSCEPTIBILITY BY COUNTRY IN CENTRAL AMERICA OR MEXICAN STATE. Letters after hosts represent the following countries or states: Ox—Oaxaca; Ch—Chiapas; Gt—Guatemala; Bz—Belize; Hn—Honduras; Es—El Salvador; Nc—Nicaragua. [1] Based on report in Hawksworth and Wiens (1996). [2] *Pinus pseudostrobus* var. *apulcensis* is a synonym for *Pinus oaxacana* in Farjon and Styles (1997). [3] First report on this host. For other reported hosts see Hawksworth and Wiens (1996). [4] Several species of pines have been reported as hosts for this dwarf mistletoe by Hawksworth and Wiens (1996). [5] *Pinus rudis* is a synonym for *Pinus hartwegii* in Farjon and Styles (1997). [6] Based on report in Geils and Vazquez Collazo (2002).

| Mistletoe	Principal pine hosts	Other pine hosts	Immune pines
Arceuthobium hawksworthii	*Pinus caribaea* var. *hondurensis* Bz, Hn	*Pinus tecunumanii* Bz	
Arceuthobium hondurense	*Pinus oocarpa* Hn, (Es?)[1] *Pinus tecunumanii* Ox, Ch, Hn (Gt?)[1]	*Pinus maximinoi* (Hn?)[1]	*Pinus pseudostrobus* Ch
Arceuthobium aureum subsp. *aureum*	*Pinus maximinoi* Ch, Gt	*Pinus montezumae* (Gt?)[1] *Pinus pseudostrobus* and var. *apulcensis*[2] (Gt?)[1] *Pinus oocarpa* (Gt?)[1]	
Arceuthobium aureum subsp. *petersonii*	*Pinus maximinoi* Ch[3] *Pinus pseudostrobus* Ox, Ch *Pinus pseudostrobus* var. *apulcensis* Ch *Pinus montezumae* Ch	*Pinus devoniana* Ch *Pinus oocarpa* (Ch?)[1] *Pinus patula* (Ch?)[1]	*Pinus tecunumanii* Ch
Arceuthobium globosum subsp. *grandicaule*	*Pinus hartwegii* (*rudis*)[5] Ox, Ch, Gt, Bz *Pinus pseudostrobus* Ch, Gt	*Pinus* spp.[4]	*Pinus ayacahuite* var. *ayacahuite* Ch *Pinus tecunumanii* Ch
Arceuthobium guatemalense	*Pinus ayacahuite* Ox, Ch, Gt		*Pinus pseudostrobus* Ch
Psittacanthus pinicola	*Pinus caribaea* var. *hondurensis* Bz, Hn, Nc	*Pinus tecunumanii* Bz *Pinus oocarpa* Hn	
Psittacanthus angustifolius	*Pinus oocarpa* Ch, Bz, Hn, Es, Nc	*Pinus tecunumanii* Ch, Hn *Pinus maximinoi* Hn *Pinus caribaea* var. *hondurensis* Hn	
Struthanthus deppeanus	*Pinus pseudostrobus* and var. *apulcensis* Ch, Gt *Pinus oocarpa* Ch, Bz, Hn *Pinus maximinoi* Ch, Gt, Hn	*Pinus montezumae* Ch *Pinus tecunumanii* Ch *Pinus devoniana* Ch *Pinus patula*[6] Ox, Ch	
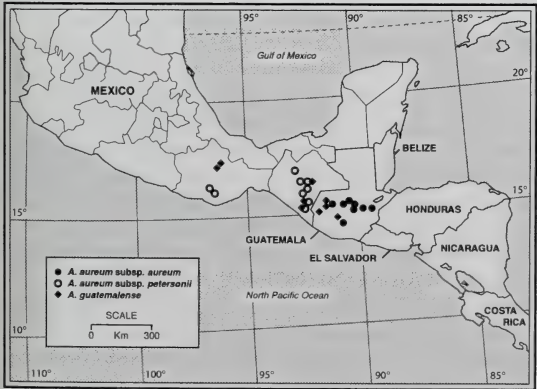
FIG. 2. Distributions of *Arceuthobium aureum* subsp. *aureum* and subsp. *petersonii* and *A. guatemalense*.

primarily south and west of Coban (Departments Alta Verapaz, El Quiche, and Zacapa) (Hawksworth and Wiens 1977, 1996) (Fig. 2).

In Guatemala, its principal host is *Pinus maximinoi* (Mathiasen et al. 1999) and not *P. pseudostrobus* as reported by Hawksworth and Wiens (1977, 1996) (Table 1). Although Hawksworth and Wiens (1977, 1996) reported this dwarf mistletoe does not form witches' brooms, it frequently causes the formation of witches' brooms on severely infected *P. maximinoi* (Mathiasen et al. 1999). Although we have attempted to find this dwarf mistletoe parasitizing other pines in Guatemala as reported by Hawksworth and Wiens (1977, 1996) (e.g., *P. pseudostrobus*, *P. pseudostrobus* Lindl. var. *apulcensis* (Lindl.) G. R. Shaw (reported as *P. oaxacana* Mirov in Hawksworth and Wiens 1996), and *P. montezumae* A. B. Lambert), we have been unable to do so. In addition, closely associated *Pinus oocarpa* growing near severely infected *P. maximinoi* were not infected in Guatemala. There-

fore, we do not agree with the report of Hawkworth and Wiens (1977, 1996) of *P. oocarpa* as a principal host for this dwarf mistletoe in Guatemala. If this mistletoe occurs on *P. oocarpa,* it is uncommon.

Arceuthobium aureum Hawksw. & Wiens subsp. petersonii Hawksw. & Wiens

Arceuthobium aureum subsp. *petersonii* is distributed in Chiapas and Oaxaca, Mexico (Hawksworth and Wiens 1977, 1996) (Fig. 2). Although we have been unable to locate the populations of this dwarf mistletoe collected near Porvenir and Siltepec, Chiapas (Hawksworth and Wiens 1996), we found a population of this dwarf mistletoe west of Motozintla de Mendoca, Chiapas on Mexico Route 200 at an elevation of 1700 m (Fig. 2). This is well below the lower elevational limit of 2200 m reported for *Arceuthobium aureum* subsp. *petersonii* by Hawksworth and Wiens (1977, 1996). The host at this location was *Pinus maximinoi.* Although the plants of this mistletoe population were smaller than reported for *Arceuthobium aureum* subsp. *petersonii* by Hawksworth and Wiens (1977, 1996), based on the morphology and phenology of these populations we have tentatively classified this population as *Arceuthobium aureum* subsp. *petersonii.* A second population of *Arceuthobium aureum* subsp. *petersonii* was found on *P. maximinoi* approximately 4 km south of Pueblo Nuevo Sichuatepec (Fig. 2). *Pinus oocarpa* growing near severely infected *P. maximinoi* were not infected at this location, so we conclude that *P. oocarpa* is less susceptible to this mistletoe than reported in Hawksworth and Wiens (1996) (Table 1). This is the first report of *Arceuthobium aureum* subsp. *petersonii* on *P. maximinoi.* Large witches' brooms are induced on this host.

The principal hosts of *Arceuthobium aureum* subsp. *petersonii* in Chiapas are *Pinus pseudostrobus, P. pseudostrobus* var. *apulcensis* (*P. oaxacana*), *P. montezumae* (Hawksworth and Wiens 1977, 1996), and *P. maximinoi.* We agree with Hawksworth and Wiens (1996) that *Pinus devoniana* Lindl. is less susceptible to *Arceuthobium aureum* subsp. *petersonii* and should be classified as a secondary host. Hawksworth and Wiens (1977, 1996) reported this dwarf mistletoe on *P. patula* from Chiapas, but we have not observed this mistletoe on *P. patula* there. The principal host of this dwarf mistletoe in Oaxaca is *P. pseudostrobus,* but it has also been collected there on *P. devoniana* (reported as *P. michoacana* Martinez; Hawksworth and Wiens 1977, 1996).

Arceuthobium guatemalense Hawksw. & Wiens

Arceuthobium guatemalense is one of the rarest dwarf mistletoes in Central America and southern Mexico (Hawksworth and Wiens 1972, 1996). However, we have now discovered additional pop-
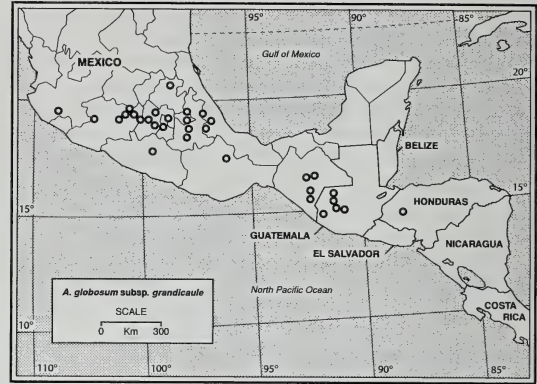

FIG. 3.   Distribution of *Arceuthobium globosum* subsp. *grandicaule.*

ulations of this mistletoe in western Guatemala and southwestern Chiapas (Fig. 2). We have found two populations in Department San Marcos, Guatemala, one approximately 12 km south of Ixchiguatan and another population 12 km east of Sidotol. Our attempts to find this dwarf mistletoe at the type locality designated by Hawksworth and Wiens (1972) have been unsuccessful because most of the *Pinus ayacahuite* var. *ayacahuite* at the type local have been harvested. We have also discovered additional populations in the vicinity of Porvenir in southwestern Chiapas (Fig. 2). *Arceuthobium guatemalense* is common in this area.

We have not found this dwarf mistletoe parasitizing the other common soft pine in southern Mexico, *P. strobus* L. var. *chiapensis* Martinez, so the only reported host for *Arceuthobium guatemalense* remains *P. ayacahuite* (Hawksworth and Wiens 1996) (Table 1).

Arceuthobium globosum Hawksw & Wiens subsp. grandicaule Hawksw. & Wiens

Arceuthobium globosum subsp. *grandicaule* is a common parasite of several species of pines in central Mexico (Hawksworth and Wiens 1977, 1996) (Fig. 3). It is also known from western Guatemala (Hawksworth and Wiens 1977, 1996) and has recently been reported from western Honduras parasitizing *Pinus hartwegii* Lindl. in Celaque National Park (Melgar et al. 2001b) (Fig. 3). We have also located several populations of this dwarf mistletoe in Chiapas, Mexico (Fig. 3). It is common in the Sierra Madre de Chiapas at high elevations near Porvenir and Canada in southwestern Chiapas. We have also found two populations near San Cristobal de las Casas in central Chiapas (Fig. 3).

The principal host of *Arceuthobium globosum* subsp. *grandicaule* in Chiapas is *Pinus pseudostrobus* (Table 1). Several large trees of both *Pinus tecunumanii* and *P. ayacahuite* Ehrenb. ex Schlecht. var. *ayacahuite* growing near severely infected *P. pseudostrobus* were not infected at several loca-
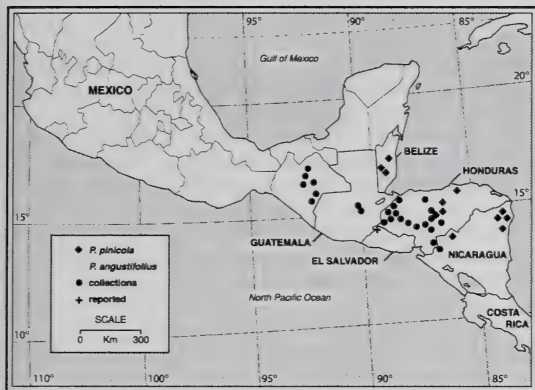
Fig. 4.   Distributions of *Psittacanthus angustifolius* and *P. pinicola.*

tions in Chiapas. Therefore, these pines are classified as immune to *Arceuthobium globosum* subsp. *grandicaule* (Table 1). The principal hosts of this dwarf mistletoe in Central America are *Pinus hartwegii* (reported as *Pinus rudis* Endl. in Hawksworth and Wiens 1977, 1996) and *Pinus pseudostrobus.*

LORANTHACEAE

Psittacanthus angustifolius Kuijt

The most common and widespread mistletoe on pines in Central America is *Psittacanthus angustifolius* (Mathiasen et al. 1998; Beatty et al. 1999; Mathiasen et al. 2000b). This common mistletoe occurs throughout most of Honduras (Fig. 4), but it was originally described from Nicaragua (Kuijt 1987). It is also common in the pine forests of central Guatemala south of Coban (Departments Alta Verapaz and Baja Verapaz) and in central Chiapas, Mexico (near the villages of Pueblo Nuevo Sichuatepec and Jitotol) (Mathiasen et al. 2000c) (Fig. 4). We have also observed this mistletoe in Monte Cristo National Park in northwestern El Salvador (Fig. 4). The mistletoe is common there on *Pinus oocarpa,* but we were unable to collect it because of restrictions on removing plants from the National Park. It is probably common in the pine forests of El Salvador and Nicaragua.

This mistletoe parasitizes several species of pines (Table 1), but it is most common on *Pinus oocarpa* (Beatty et al. 1999). It probably parasitizes both *P. oocarpa* and *P. maximinoi* in Nicaragua since these are the only two common, high elevation pines there and both of these pines are parasitized in Honduras (Mathiasen et al. 2000b). It has recently been reported on *Pinus caribaea* var. *hondurensis* in north-central Honduras, but how common this mistletoe is on this host is unknown (Mathiasen et al. 2002a). It is probable that this mistletoe also parasitizes *P. caribaea* var. *hondurensis* in Nicara-

gua. This mistletoe has been reported on hosts other than pines in Honduras (Melgar et al. 2001a), but this is evidently a rare occurrence. It has been reported on oak (*Quercus* sp.) from Chiapas (Kuijt unpublished), but our attempts to find this mistletoe on oaks in Mexico, Honduras, and Guatemala have been unsuccessful.

Psittacanthus pinicola Kuijt

Thus far, this mistletoe has been reported parasitizing pines in Belize, Honduras, and Nicaragua (Kuijt 1987) (Fig. 4). Our attempts to find it parasitizing hosts other than pines have been unsuccessful. Its principal host is *Pinus caribaea* var. *hondurensis,* but we have also found it parasitizing *Pinus tecunumanii* in Belize and *P. oocarpa* in Honduras (Beatty et al. 1999) (Table 1). It undoubtedly parasitizes other pines in Central America, but whether or not it occurs on hardwoods remains unknown. It is probable that this mistletoe only parasitizes pines in Central America (Kuijt 1987).

Psittacanthus schiedeanus (Cham. & Schlecht.) Bl.

Psittacanthus schiedeanus is the most commonly reported mistletoe on pines in Central America (Vasquez Collazo et al. 1982; Scharpf et al. 1997). However, specimens of this mistletoe on pines deposited at the herbaria we have visited in Central America (ESNACIFOR, EPAM, NHON) were all specimens of *Psittacanthus angustifolius.* Since many investigators used A Flora of Guatemala (Standley and Steyermark 1946) for identifying species of *Psittacanthus* in Central America, mistletoes of this genus occurring on pines were consistently classified as *P. schiedeanus* because *P. angustifolius* was not described as a separate species until 1987 (Kuijt 1987). We have yet to observe *P. schiedeanus* on pines in Central America or Mexico. Because all of the herbarium specimens we have examined for this species collected on pines were *P. angustifolius,* we conclude *P. schiedeanus* probably does not occur on pines in Central America or southern Mexico. If it does infect pines, it is not a common parasite of this genus based on our field observations and inspection of herbarium specimens. However, this mistletoe has been reported to be common and damaging on pines in Michoacan, Mexico (Vazquez Collazo et al. 1982; Vazquez Collazo and Geils 2002).

Struthanthus deppeanus (Cham. & Schlecht.) Bl.

This mistletoe rarely parasitizes pines in Honduras and Guatemala, but it is common in Chiapas, Mexico (Fig. 5). In Honduras, it is only known from *Pinus oocarpa* (Table 1), but it probably occurs on other pines. However, our extensive surveys for mistletoes on pines in Honduras have only uncovered four locations where this mistletoe occurs there (Fig. 5). This mistletoe is also uncom-
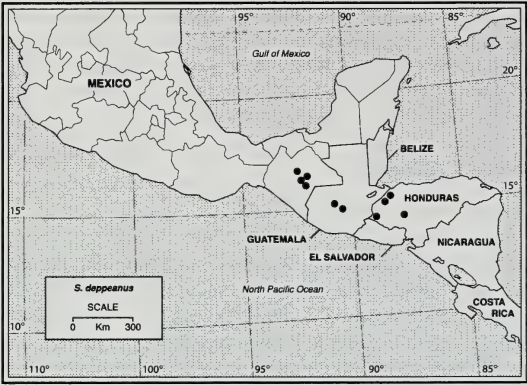
Fig. 5. Distribution of *Struthanthus deppeanus*.

mon in Guatemala; our surveys there have only found two locations for this mistletoe there.

In Guatemala this mistletoe has been found on *Pinus maximinoi* and *P. pseudostrobus* var. *apulcensis* (*P. oaxacana*) (Table 1). We have also found it in Guatemala on *Casaurina equisetifolia* L. ex J. R. & G. Farst. In Chiapas this mistletoe is common in the pine forests near San Cristobal de las Casas and the villages of Jitotol and Pueblo Nuevo Sichuatepec (Fig. 5). It also has a much larger host range in Chiapas occurring on *Pinus oocarpa, P. maximinoi, P. tecunumanii, P. pseudostrobus, P. pseudostrobus* var. *apulcensis* (*P. oaxacana*), *P. montezumae,* and *P. devoniana* (*P. michoacana*) (Table 1). Although this mistletoe has been reported on *P. patula* in Oaxaca and Chiapas (Chazaro and Oliva 1988; Geils and Vazquez Collazo 2002), we have not observed it on this host in southern Mexico.

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REGIONAL- AND LOCAL-SCALE VARIATIONS IN PLANT DISTRIBUTION IN THE SONORAN DESERT

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ABSTRACT

This study documents dominant woody species cover at 30 locales throughout the northern Sonoran Desert in order to observe distributional patterns and associations among taxa at the regional scale. Factor analysis revealed two main findings: first, although common taxa are broadly distributed over the same areas in the northern Sonoran Desert, species associations can be statistically distinguished locally; second, after factor analysis, *Carnegiea gigantea* density loaded highly (0.934) on the same factor with two of its common nurse species, *Ambrosia deltoidea* (0.843) and *Olneya tesota* (0.836), but not with *Cercidium microphyllum* (0.139), also a common nurse. This suggests that available cover alone does not explain the observed *Carnegiea gigantea* patterns.

Key Words: *Ambrosia*, Arizona, *Carnegiea gigantea*, *Cercidium microphyllum*, *Larrea tridentata*, *Olneya tesota*, saguaro, Sonoran Desert.

Species distributions are patchy at all scales (e.g., Erickson 1945), however, at the global or regional scale, a broad boundary marks the edge of the range of most species. *Ambrosia deltoidea* (Torr.) Payne (bursage, Asteraceae, shrub), *A. dumosa* (A. Gray) Payne (bursage, Asteraceae, shrub), *Carnegiea gigantea* (Engelm.) Britt. & Rose (saguaro, Cactaceae, columnar cactus), *Cercidium microphyllum* (Torr.) Rose & Johnston (palo verde, Fabaceae, tree), *Larrea tridentata* (DC.) Coville (creosote, Zygophyllaceae, shrub), *Olneya tesota* Gray (ironwood, Fabaceae, tree) and *Prosopis* spp. (mesquite, Fabaceae, tree), are among the most common and widespread taxa found in the Sonoran Desert (Turner and Brown 1994). At the regional scale, the distributions of these taxa almost entirely overlap in Arizona (Turner et al. 1995). Locally, upper bajada slopes support *C. microphyllum, A. dumosa, L. tridentata, O. tesota* and *C. gigantea,* whereas *A. deltoidea* and *Prosopis* have been observed throughout the bajada (Phillips and MacMahon 1978). Another single-locale study classified *A. deltoidea, L. tridentata, C. gigantea, Prosopis,* and *A. dumosa,* into a "bajadas and washes" group; however, *C. microphyllum* and *O. tesota* were not classified into any of the groups (Parker 1988). These taxa serve as *C. gigantea* nurse plants, which recruit most successfully under the canopy of a nurse (e.g., Turner et al. 1966; Franco and Nobel 1989).

This study aims 1) to determine local distribution trends among widely distributed Sonoran Desert species, sampling in 30 locales over 50,000 square kilometers of the Sonoran Desert, and 2) to determine if such distributions are associated with *C. gigantea* population densities over Arizona. This study seeks to make preliminary observations about regional scale distributional patterns.

The data were collected as part of a larger study of *C. gigantea* (Drezner 2003). Percent cover data were collected (about 20–25 measurements per species) for the species listed above in 30 locations (Fig. 1). All species with percent cover values less than 1% were assigned a 1% cover value. All plots were flat and washes were excluded (McAuliffe 1984). Site selection was based on *C. gigantea* presence; other species were not considered. Plot size ranged from 345 m² to 11,300 m² depending on *C. gigantea* densities, which were quota sampled (e.g., Brum 1973) (n = 15, 20 in larger populations). Nine variables were computed (Table 1), including density of *C. gigantea* less than one meter in height to represent youth. Factor analysis (principal component analysis extraction method) was conducted with Varimax rotation using *SPSS 10.1* software, and factors with eigenvalues less than one were excluded.

Four factors had an eigenvalue of more than one, cumulatively explaining over 83% of the total variance (Table 2). Despite the common to ubiquitous nature of the taxa regionally, local-scale statistical associations between some species and not others were observed. That each variable is best represented by only one of the factors (i.e., the next highest loadings are substantially lower) reflects the distinctiveness of each of the species guilds and associations established in this analysis. The *C. gigantea, O. tesota,* and *A. deltoidea* variables loaded highly on the first factor (Table 1). These species are more abundant in the east and southeast than in other areas. *Carnegiea gigantea* is often associated with the latter as they are common nurse plants (Suzan et al. 1996; Drezner and Garrity in press); thus the first factor is called "*C. gigantea.*" *Cercidium microphyllum* had the highest loadings on
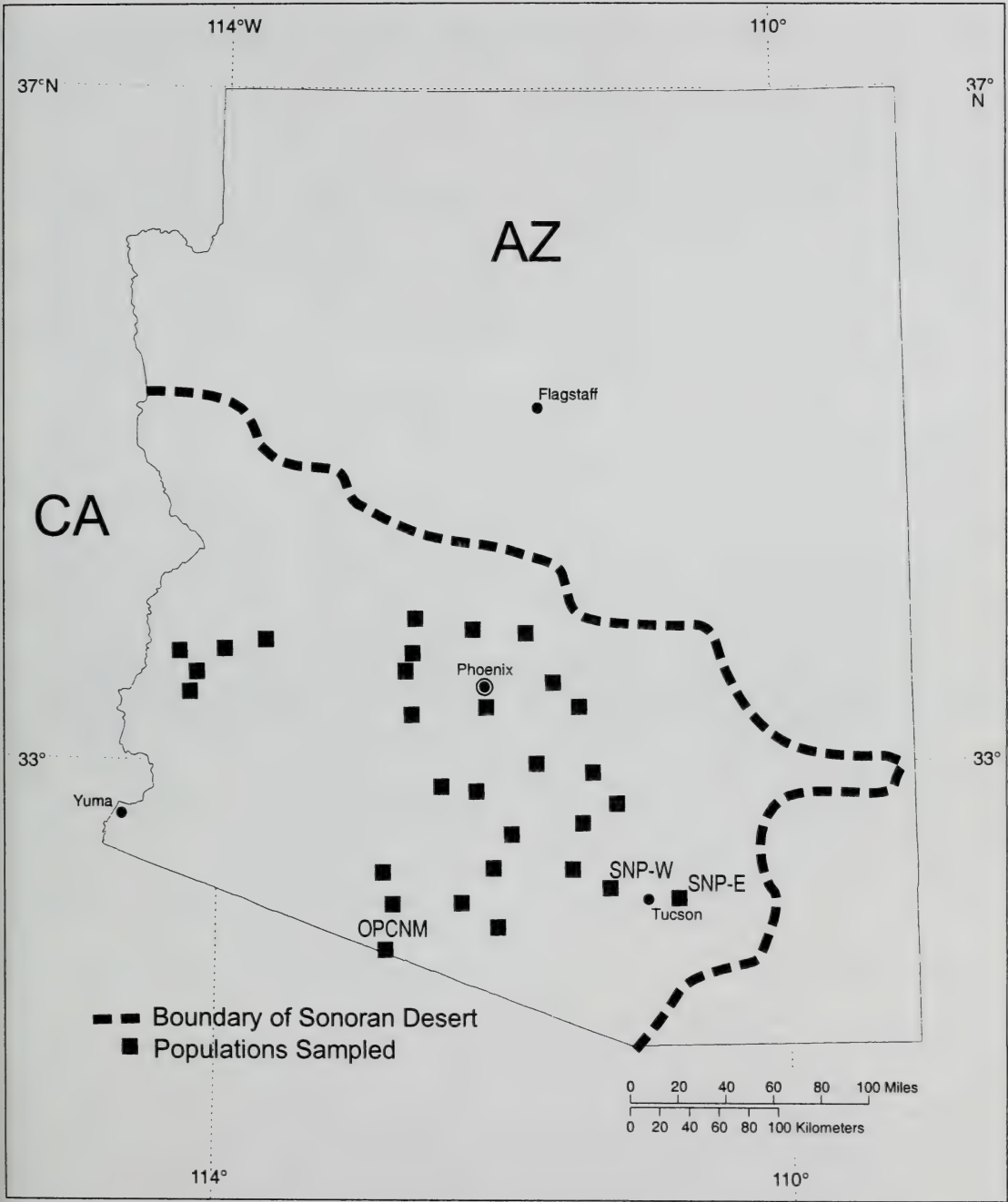
FIG. 1.   The location of the 30 study locales. Modified from Turner et al. (1995).

its own factor (called *C. microphyllum*), suggesting that its distribution is unlike that of any of the other species. *Ambrosia deltoidea* had loadings of over 0.3 on the *C. microphyllum* factor (Table 1). This may reflect the higher establishment success of *C. microphyllum* under cover of nurse plants such as *A. deltoidea* (McAuliffe 1988).

Ambrosia dumosa and dead *C. microphyllum*

loaded highly on the third factor (named *dry/west*) (Table 1). Dead *C. microphyllum* individuals were more common in the relatively arid, western portions of the study area, though premature mortality has been observed in other parts of the Sonoran Desert (Bowers and Turner 2002). *Carnegiea gigantea* has shallower roots than their *C. microphyllum* nurses, sometimes leading to the premature

TABLE 1. FACTOR ANALYSIS, BEFORE (TOP) AND AFTER (BOTTOM) VARIMAX ROTATION. An asterisk (*) denotes the highest loading for each variable. Abbreviations: cover of *Ambrosia deltoidea* (*Adel*), *A. dumosa* (*Adum*), *Cercidium microphyllum* (*Cmic*), *Larrea tridentata* (*Ltri*), *Olneya tesota* (*Otes*), *Prosopis* spp. (*Prsp*), and density of *Carnegiea gigantea* (*Cgig*).

	1 (Cgig)	2 (Ltri–Prsp)	3 (Dry/West)	4 (Cmic)
Unrotated Component Matrix				
Adel	0.931*	0.078	−0.047	0.116
Adum	−0.307	0.713*	0.471	0.116
Cmic-dead	−0.166	0.168	0.881*	0.175
Cmic-total	0.367	0.252	−0.306	0.780*
Ltri	−0.469*	0.485*	−0.352	−0.332
Otes	0.698*	0.168	0.226	−0.443
Prsp	0.056	−0.750*	0.377	0.079
Cgig density	0.953*	0.135	0.034	0.056
<1 m Cgig density	0.941*	0.112	0.073	−0.135
Rotated Component Matrix (Varimax Rotation)				
Adel	0.843*	0.139	−0.142	0.373
Adum	−0.101	−0.399	0.816*	0.047
Cmic-dead	−0.044	0.278	0.879*	−0.104
Cmic-total	0.139	−0.042	−0.041	0.937*
Ltri	−0.291	−0.748*	−0.041	−0.207
Otes	0.836*	−0.023	0.059	−0.246
Prsp	−0.075	0.818*	−0.045	−0.191
Cgig density	0.934*	0.083	−0.085	0.214
<1 m Cgig density	0.944*	0.094	−0.078	0.123

death of *C. microphyllum* individuals (Vandermeer 1980; McAuliffe 1984, 1988), presumably more pronounced in drier regions. This relationship has been likened to a predator-prey cycle (Vandermeer 1980). More abundant in the west, *Ambrosia dumosa* also loaded highly on this factor. The *dry/west* factor may reflect the more arid Lower Colorado River Valley subdivision of the Sonoran Desert (Turner and Brown 1994). *Larrea tridentata* (negative) and *Prosopis* had the highest loadings on the second factor (*L. tridentata-Prosopis*). Where one tends to be found, the other tends to be absent or nearly so, and this factor may also reflect species diversity (higher with *Prosopis*, lower with *L. tridentata*).

The second observation of this study suggests that high-density *C. gigantea* populations are associated with certain species. Although *C. microphyllum* is an important nurse for *C. gigantea* (e.g., Vandermeer 1980), areas with the highest *C. gigantea* densities do not follow *C. microphyllum* distributional patterns; rather, they follow *O. tesota* and

A. deltoidea. Parker (1988) also classified *C. microphyllum* and *C. gigantea* into different groups based on their distribution. Parker (1988) grouped *C. gigantea* with *A. deltoidea* and *L. tridentata,* although *L. tridentata* is a relatively ineffective *C. gigantea* nurse (Hutto et al. 1986; Parker 1989). *Ambrosia deltoidea* and *O. tesota* densities are relatively high in areas with high summer precipitation and cooler summer temperatures, factors that are also critical for *C. gigantea* regeneration (Steenbergh and Lowe 1983) and presumably contribute to their higher densities in these areas (Turner et al. 1995). *Carnegiea gigantea* density does not appear to be related only to available nurse cover, but also to species composition or abiotic environmental variables.

This study demonstrates that spatial separation within overlapping ranges of different taxa warrants further attention in the Sonoran Desert. Other studies have documented patterns locally (Phillips and MacMahon 1978; Parker 1988). In this study, species associations were observed regionally. While all of these species are very common throughout the northern Sonoran Desert, I found that individuals of some species co-exist together locally, while other species associations exhibit different spatial patterns across the region.

TABLE 2. EIGENVALUES AND VARIANCE EXPLAINED BEFORE AND AFTER VARIMAX ROTATION.

Factor	Initial eigenvalues			Rotation sums of squared loadings		
	Total	% var	Cum %	Total	% var	Cum %
1	3.628	40.3	40.3	3.294	36.6	36.6
2	1.462	16.2	56.6	1.503	16.7	53.3
3	1.417	15.7	72.3	1.480	16.4	69.7
4	1.001	11.1	83.4	1.230	13.7	83.4

Molly Davies and the Arizona State University Office of Climatology for use of field equipment. I thank Barbara Trapido-Lurie for help with the map and two anonymous reviewers for helpful suggestions.

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REVIEWS

Orchids and their conservation. By Harold Koopowitz. 2001. Timber Press, Portland, OR. 176 pp. ISBN 0-88192-526-8.

There are few plant groups that by their mere mention can elicit visions of rarity, and orchids among them are supreme. Why this is the case is anybody's guess. The orchid family has been wrapped in a quilt of classiness, romance, intrigue, adventure and fantasy. Even today, orchid fever establishes new standards of lunacy as we witness the unfolding of the *Phragmipedium kovachii* story. Excessive greed adds spice as inflated egos battle one another over a recently discovered, rather unusual "phrag", an ugly species with excessively large, floppy, flowers (Holden 2002).

The Orchidaceae is one of the most species rich families of flowering plants. It certainly would be an intriguing analysis to determine whether or not there are proportionately more rare orchids than, say, rare species of grasses or comps. Regardless of the outcome of any such analysis, there are ample rare, endangered or threatened species of orchids. For every rare, horticulturally important taxon, there must be plenty of obscure, inconspicuous species. Why are these orchids rare? It is not difficult to conjure a plethora of reasons. Excessive collection is the one we tend to blame the most but with few exceptions, it may be significant only for some marquee species. Habitat destruction obviously has affected many species, orchids or otherwise. Mixed among these situations is the notion that rarity is natural and not necessarily bad. It may actually offer an advantage as Rabinowitz (1981) revealed for some grasses. For orchids, rarity is well integrated in their pollination biology and likely has played a major role in diversification (Ackerman 1986; Tremblay and Ackerman 2001). All these issues need to be considered in any approach to conservation of orchid species.

Orchids and their conservation by Harold Koopowitz is a timely book. Orchidists throughout the world are recognizing that their hobby is threatened by the very things that make it attractive. Meanwhile, most of the larger orchid societies have conservation committees, and some, like the San Diego Orchid Society, have been quite effective in promoting research and education in orchid conservation. Now there is a single source whereby one can be introduced to orchid biology and be presented with an integrative account of conservation in the family. The IUCN's Orchid Action Plan (1996) covers much of the same territory, but it is rather dry reading and not nearly as attractively produced as *Orchids and their conservation*.

Harold Koopowitz is well known among orchid circles; he circulates among horticulturalists as easily as among biologists. His experience as a scientist, orchidist, and conservationist lends some degree of authority to *Orchids and their conservation.* The book logically begins with orchid biology and progresses to population ecology en route to a number of conservation topics. One of the more interesting chapters is "The Continuing Need for Orchid Species" where Koopowitz explains the importance of a vibrant species pool to the horticultural trade, a theme that hits hard to both the breeder and hobbyist. Another insightful chapter, "Conservation and Commercialism", touches on the crass exploitation of the past and present, and the operations of responsible orchid nurseries of today. Stories of deforestation, impending doom, bureaucratic bungling, and conservation successes and failures pepper the other chapters.

CITES, the Convention on International Trade in Endangered Species, has been a sore point to the orchid world. Koopowitz explains the history and issues and relates how some view the inclusion of orchids on CITES to be a house of horrors for both orchid research and conservation. As in most bureaucracies, CITES has taken on a life of its own and there seems to be no antidote short of nuclear fission.

A scientist can fault the paucity of references, or the at-times lackadaisical accounting of the biology of orchids. Some of us may also be annoyed when Koopowitz states, "Its time for orchid biologists to start gathering the information that we need to carry out effective conservation" when the handful of these specialists have been doing just that for decades. And if one reads through the text from cover-to-cover, then you will find repetitious sections and misspelled names (people, not plants!). Although the author claims that "orchids merely represent a model that allows one to understand events that threatened general biodiversity," this book seems to emphasize the uniqueness of orchids, rather than the commonality of their situation. After all, the author's experience in conservation is largely drawn from orchids, and whether by design or not, the book addresses the needs of the concerned orchidist more than anybody else.

As an orchid biologist myself, I found the chapters most remote from my experience to be the most interesting. Perhaps an orchidist would see it that way as well.

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A flora of Glacier National Park, Montana. By Peter Lesica with illustrations by Debbie MacNeil. 2002. Oregon State University Press, Corvallis, OR. 512 pp. Softcover $32.95. ISBN 0-87071-538-0.

Glacier National Park, straddling the spine of the North American continent in northwestern Montana, is one of the crown jewels of the National Park System. Meadows of blooming beargrass (*Xerophyllum tenax*) with jagged mountain peaks in the background epitomize this portion of the Rocky Mountains, and have attracted the attention of botanists since before Glacier's designation as a national park in 1910. Millions of visitors from around the world have been drawn to the park, in part, because of the spectacular wildflowers. The publication of a new flora for Glacier National Park provides an up-to-date treatment of the park's flora, which surprisingly has not been covered with a comprehensive floristic treatise since Standley's 1921 Flora of Glacier National Park, Montana. This new work builds on the checklists that Peter Lesica had published earlier, and represents the culmination of an eighteen-year project.

The flora begins with an introductory section that includes a brief description of the park, followed by a discussion of the climate and geology. The author uses a three-zone classification to describe the distribution of plants in the park: montane, subalpine (upper and lower), and alpine. Detailed descriptions of each of the zones follow, with information on common vegetation types such as grasslands, riparian forests, aspen, and fellfields. Included in the information provided are lists of common species that characterize particular vegetation types. A detailed history of the botanical exploration of the park and associated publications is provided, though this discussion would have been strengthened if the author had investigated more regional collections. The herbarium at Montana State University (MONT) contains, for example, collections made in Glacier by P. A. Hawkins from 1920 that

deserve mention. Completing this section is a synopsis of the flora, discussion of the floristic plant geography, and an examination of the portion of the flora that is introduced. The author is obviously fascinated with the sources of the flora and the association of plants of certain floristic affinities with various life zones, and has attributed the species in the flora into four broad geographic patterns (cordilleran, boreal, arctic-alpine, and Great Plains). Regrettably, the author didn't include his analysis of the affinities of each species in the individual species descriptions, perhaps due to constraints on the length of the publication. The introductory section also includes a discussion on how to use the book including a brief introduction to using taxonomic keys, comments on taxonomic philosophy, a glossary, and an extensive reference list.

The heart of the book, of course, is the floristic treatment. Keys are provided to the 86 families, 345 genera, and 1132 species that have been verified to occur within the park. Included in the treatment is information about family and generic characters, along with a brief description of each plant followed by information about habitat, its distribution within the park including whether east and/or west of the continental divide, and the overall species distribution. Infraspecific taxa are included when recognized, with information to distinguish multiple taxa when necessary. Included in each species description is a list of synonyms used by regional and local floras, which increases the ease of use for a broad audience. A welcome addition is the occasional discussion of taxonomic problems or philosophy, though there is no mention, for example, of the difficulties in distinguishing the moonworts (*Botrychium* spp.). More discussion of this and similar problems would have made the flora even more valuable.

This flora represents a treatment designed to be useful both to the professional botanist and also by anyone who enjoys knowing the particular plant that has riveted their attention. One of the advantages of a floristic treatment of a relatively small area is that the keys can be much simpler than in a regional flora. Lesica's keys emphasize easy to understand characters that will normally allow the reader to separate species, and are generally quite brief. One could quibble that a few of the keys are too simple and will not always separate difficult species, but these keys would be appropriate for use in a beginning course on wildflowers, and professionals can always refer to the more rigorous literature. The book includes 351 original line drawings by Debbie McNeil of the common species encountered in the park, with an emphasis on illustrating different genera. These excellent illustrations provide information that facilitates the use of the book by a wide spectrum of plant aficionados. Regretfully, the line drawings are not as sharp as it appears the original drawings may have been, perhaps due to the reduction in size of the illustrations in

order to fit several onto one page. The presence of information on the reduction or magnification scale of the line drawings would have been helpful, especially to new enthusiasts or amateur users, as the same page may contain similar size drawings illustrating plants of very disparate sizes. There are also eight pages of color photographs by the author in the center of the book that highlight some of the spectacular wildflowers of the park, adding to the appeal of the book for a broad audience.

In a work of this magnitude, there will always be a few errors, but this flora has remarkably few typographical errors and other problems and has an excellent index. Only one species, *Epilobium pygmaeum* (Speg.) Hock and Raven, was found to be missing in the species keys, and I noticed only one key that was misnumbered. This book represents a work that will be enjoyed, and will benefit everyone—from wildflower enthusiasts, to National Park Service personnel, to professional botanists. Anyone interested in plants who plans on traveling to Glacier National Park or the nearby Rocky Mountains would be remiss if they failed to acquire this book prior to or during their visit.

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ANNOUNCEMENTS

VERNAL POOL VEGETATION OF CALIFORNIA: VARIATION WITHIN POOLS

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Abstract

Existing classifications of Californian vernal pools are based on whole-pool samples, which do not reflect the internal heterogeneity of vegetation within pools. We adopted a sampling scale finer than that of entire pools, using plots of 10 m^2 placed in visually homogenous zones inside pools. Our analysis was based on >700 plots in >200 pools from 21 locations within northern California's Central Valley and Sierra Nevada foothills. Sixteen community types, each with a unique floristic composition, were recognized. We showed that a given vernal pool may consist of more than one community type, the same community type can be encountered in different pools, and most community types are locally restricted to a single vernal pool region, only a few having a wider geographical range. The presence of rare species was linked with particular community types. The implication of these results is that conservation and mitigation measures must be locally focused. Our data demonstrated that the whole pools consist of a complex of autonomous plant communities, thus changing our perception of vernal pool vegetation. California vernal pools differ from European ephemeral wetlands in the presence of many endemic genera (e.g., *Downingia, Lasthenia, Navarretia, Plagiobothrys, Pogogyne, Psilocarphus*). Their vegetation is recognized as the new class *Downingio bicornutae-Lasthenietea fremontii.*

Key Words: Great Central Valley, class *Downingio-Lasthenietea,* ephemeral vegetation classification, Braun-Blanquet approach, sampling methods, rare species, vegetation heterogeneity.

Vernal pools are shallow depressions underlain with an aquatard. The depressions fill with water during the winter, then dry over the course of several spring months. While subsurface moisture remains, the (mainly native annual) species grow rapidly, flower, and produce seeds. Vernal pools are distributed throughout mediterranean-climate California mostly at elevations below 300 m. The location of pool complexes are best known for the Great Central Valley (Holland 1998), but they also occur in the Coast Ranges, Modoc Plateau, Transverse Ranges, Sierra Nevada foothills, and such coastal lowlands as the Sacramento Delta, San Luis Obispo and Santa Barbara areas, and portions of San Diego County (Keeler-Wolf et al. 1998). The

vernal pool habitat is one of the few in those parts of California that is still dominated by native plant taxa (Holland and Jain 1988). Furthermore, the taxa are largely endemic to vernal pools, and a number are listed as threatened/endangered. Keeler-Wolf et al. (1998) and Keeley and Zedler (1998) estimated that >100 taxa are either restricted to vernal pools or are most commonly found in vernal pools. Approximately 90% are native and 55% have ranges entirely within the state of California (Holland 1976; Keeler-Wolf et al. 1998).

Vernal pool landscapes continue to be converted to agriculture or urban housing tracts. We do not know exactly how much vernal pool area has been lost in the last 200 yr, but estimates based on soil maps, the presence of relict pools, and inference suggest a loss of 60–90% (Holland 1978).

Major reviews of the environmental factors that appear to drive the distribution of individual species and species assemblages, such as water chemistry, soil series, geologic substrate, and regional climate, include those by Nikiforoff (1941), Jain (1976), Jain and Moyle (1981), Holland and Jain (1981a, b, 1988), Zedler (1987), Ikeda and Schlising (1990), Owenby and Ezell (1992), Hobsen and Dahlgren (1998), Keeler-Wolf et al. (1998), Witham et al. (1998), Bauder (2000), Ferren et al. (1995), Fiedler and Ferren (1999), and Renshaw (2000). At a local scale, the color masses of dominant species at peak flowering indicate a zonation of vegetation within a single pool. The vegetation within a single pool is not homogeneous. A number of studies (e.g., Ko-

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Fig. 1. Locations where vernal pools were sampled. Numbers from 1 to 21 correspond to those identified in Table 1. Vernal pool regions are those of Keeler-Wolf et al. (1998): I. Northeastern Sacramento Valley Region; II. Southeastern Sacramento Valley Region; III. Southern Sierra Foothills Region; IV. Solano-Colusa Region.

TABLE 1. LOCATIONAL DATA, AND GEOLOGIC/EDAPHIC INFORMATION. Geomorphic surfaces, landforms and soil series are according to Marchand and Allwardt (1981) and Helley and Harwood (1985). Vernal Pool regions (VP reg) are according to Keeler-Wolf et al. (1998): I. Northeastern Sacramento Valley Region; II. Southeastern Sacramento Valley Region; III. Southern Sierra Foothills Region; IV. Solano-Colusa Region.

VP reg.	Loc. no.	Location name	County	Eleva-tion (m)	Geomorphic surface	Landform	Soil series	N Latitude	W Longitude
I	1	Inks Creek Ranch	Tehama	328	Tuscan	mudflow terrace	Tuscan	40°,22'	122°,02'
	2	Hog Lake	Tehama	261	Tuscan	mudflow terrace	Toomes	40°,20'	122°,04'
	3	Foor Ranch	Tehama	95	Red Bluff	high terrace	Tuscan	39°,56'	122°,00'
	4	Vina Plains	Tehama	72	Red Bluff	high terrace	Tuscan	39°,54'	122°,00'
					Red Bluff	low terrace	Anita Clay		
					Modesto	incised floodplain	Berrendos		
	5	Oroville Table Mnt.	Butte	389	Lovejoy	basalt flow	Kranm-Beatsonhollow	39°,36'	121°,32'
	6	Book Farm	Butte	53	Modesto	low terrace	Tuscan	39°,39'	121°,44'
II	9	Beale AFB	Yuba	26	Riverbank	low terrace	San Joaquin	39°,05'	121°,28'
	10	Orchard Creek	Placer	35	Laguna	high terrace	Fiddyment-Kaseberg	38°,50'	121°,20'
					Modesto	floodplain terrace	Alamo-Fiddyment		
					Riverbank	low terrace	San Joaquin		
	11	Howard Ranch	Sacramento	76	Laguna	high terrace	Corning-Redding	38°,22'	121°,03'
					Valley Springs	bajada	Amador-Gillender		
					Riverbank	low terrace	Crevis Creek		
	12	Valensin Ranch	Sacramento	16	Riverbank	low terrace	San Joaquin	38°,21'	121°,18'
	14	Lane Ranch	San Joaquin	53	Laguna	high terrace	Redding	38°,14'	121°,10'
					Riverbank	intermed. terrace	Rocklin		
					Turlock Lake	terrace	Cometa		
					Riverbank	terrace	San Joaquin		
III	15	Kelsey Ranch	Merced	130	Redding	high terrace	Corning	37°,33'	120°,22'
					Redding	incised floodplain	Hornitos		
	16	Chance Ranch	Merced	145	Mehrten	strath terrace	Pentz	37°,28'	120°,25'
					Laguna	high alluv. terrace	Redding		
					China Hat	old high terrace	Redding		
	17	Icord Ranch	Merced	69	Laguna	high terrace	Redding	37°,21'	120°,24'
					Modesto	incised floodplain	Bear Creek		
					Riverbed	low terrace	Keyes		
	18	Flynn Ranch	Merced	92	Riverbank	low terrace	San Joaquin	37°,10'	120°,10'
					Riverbank	floodplain	Grangeville		
	19	Kennedy Table Mnt.	Madera	709	Lovejoy	basalt flow	Hideaway	37°,06'	119°,35'
	20	Big Table Mnt.	Fresno	472	Lovejoy	basalt flow	Hideaway	37°,02'	119°,35'
	21	Friant	Fresno	133	Riverbank	low terrace	San Joaquin	36°,58'	119°,42'
IV	7	Sacramento NWR	Glenn	27	Basin	basin	Willows	39°,25'	122°,00'
					Modesto	very low terrace	Riz		
	8	Dolan Ranch	Colusa	14	Basin	basin	Willows	39°,10'	122°,10'
	13	Jepson Prairie	Solano	7	Modesto	low terrace	Antioch-San Ysidro	38°,6'	121°,50'
					Modesto	basin rim	Pescadero-Solano		
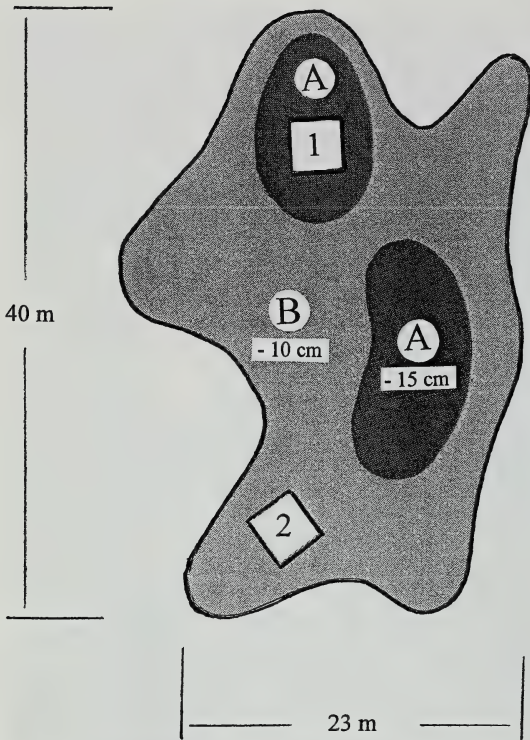
FIG. 2. Vegetation zonation within one Jepson Prairie pool (number JEP-005; 04.02.2001; GPS 10S0602911, 4237922). The location of the different polygons and of the plots are shown to scale. Polygon A occupied the deep part of the pool (−15 cm) and polygon B occupied the shallow part (−10 cm). Polygon letters and plot numbers correspond to Table 6.

pecko and Lathrop 1975; Schlising and Sanders 1982; Zedler 1987; Holland and Jain 1988; Bauder 2000) have shown that time of inundation is an important factor controlling species distribution within a pool.

The existing classification of vernal pools in *A Manual of California Vegetation* (Sawyer and Keeler-Wolf 1995) describes eight units defined on the basis of regional and geological traits, and additionally characterized by the presence of selected taxa. Their eight groups are derived from seven groups described earlier by Holland (1986). In the most recent comprehensive study, 17 vernal pool regions were defined on a geographic basis and by the presence of endemic species (Keeler-Wolf et al. 1998). These classifications are all based on whole-pool samples, which do not reflect the important, internal vegetational heterogeneity within pools. By "whole-pool samples," we mean vegetation data that has combined species growing at the outer edge with those at the bottom of a pool.

The objective of our research was to describe and classify community types repeatedly found in vernal pools of northern California, using a sampling scale finer than that of entire pools. By using this approach, we aimed to capture the diversity of species assemblages within a pool, and to reveal general patterns of community diversity and distribution.

MATERIALS AND METHODS

This paper is based on descriptions of 728 plots, each of 10 m², from more than 200 pools in 21 locations in northern California. A "location" in this paper means a single-owner parcel of land, usually several hundred hectares in area. An attempt was made to stratify locations by geologic, edaphic, and topographic categories. Superimposed on this template was the requirement that the owner would grant permission to trespass and gather data. In addition, those locations that combined several categories were preferred over those that were more simplistic, in order to maximize the efficiency of field time. Finally, the list of locations was constrained by the season's duration, the team's available field time, and the size of the budget.

The selected locations were distributed over a wide range of latitude and physical settings within the Central Valley, falling into four of Keeler-Wolf's 17 vernal pool regions (Fig. 1 and Table 1). These are the Northeastern Sacramento Valley Region, Southeastern Sacramento Valley Region, Southern Sierra Foothills Region, and Solano-Colusa Region. Elevations ranged from sea level to >700 m; landforms included basalt flows, mudflows, terraces, alluvial fan splays, and floodplains; and latitude ranged from 36°58′ to 40°22′N.

Climate is relatively uniform over all locations, with a few exceptions: Oroville (location 5) had the highest annual precipitation of any location (133.9 cm) and Kelsey, Chance, and Icord (locations 15, 16, 17) the lowest (30.5 cm). Mean annual precipitation was just under 50 cm. Mean minimum February temperatures were several degrees above freezing for all locations. Mean maximum May temperatures were also relatively uniform, averaging 26–27 C. Most locations had May precipitation-to-evaporation ratios of 0.2–0.5, indicating strongly arid conditions (Table 2).

Within a given location, the objective was to sample as many pools as possible within 1–2 days, the number of days reflecting the area of the location. We included samples within each landform/geomorphic surface/soil series unit. Arial photos and geologic and soil maps were used to delimit the units. Within each unit, there was only time to sample the first half-dozen pools encountered. There was no preference given to pools of any given area, shape, or range of depths. We sampled as many pools as we could. At small locations, all pools were sampled, while at the largest locations, 10–20% of the pools were sampled.

Each selected pool was divided into visually homogeneous polygons. The boundaries between

TABLE 2. SELECTED WEATHER DATA FOR CENTRAL VALLEY VERNAL POOL LOCATIONS. Weather station names and data are from Owenby and Ezell (1992). Precipitation/Evapotranspiration ratios (P/ET) use Feb.+May data.

Locations	Weather station	Dist. from site (km)	Elevation diff. (m)	Mean ann. temp (C)	Mean ann. precip. (cm)	Feb.+May P/ET
Inks Creek Ranch	Red Bluff	17	−245.4	17.2	56.6	0.47
Hog Lake	Red Bluff	17	−178.3	17.2	56.6	0.47
Foor Ranch	Red Bluff	25	−13.0	17.2	56.6	0.47
Vina Plains	Red Bluff	32	+72.4	17.2	56.6	0.47
Book Farm	Chico	45	+3.0	15.9	66.9	0.44
Sacramento NWR	Willows	12	+44.3	16.5	44.4	0.4
Dolan Ranch	Colusa	18	+1.5	15.8	40.3	0.33
Beale AFB	Marysville	16	−8.5	16.9	53.4	0.43
Oroville Table Mountain	Paradise	29	+144.8	15.4	133.9	0.55
Orchard Creek	Marysville	27	−17.7	16.9	53.4	0.43
Valensin Ranch	Lodi	24	−3.8	15.6	43.5	0.21
Howard Ranch	Lodi	28	−64.0	15.6	43.5	0.21
Jepson Prairie	Fairfield	2	+5.3	15.4	54.3	0.37
Lane Ranch	Lodi	25	−41.1	15.6	43.5	0.21
Kelsey	Merced	33	−82.9	16.5	30.5	0.24
Chance Ranch	Merced	17	−98.1	16.5	30.5	0.24
Icord Ranch	Merced	7	−21.9	16.5	30.5	0.24
Flynn Ranch	Merced	42	−45.6	16.5	30.5	0.24
Kennedy Table Mountain	Auberry	13	−56.4	15.9	62.6	0.21
Big Table Mountain	Auberry	12	+179.8	15.9	62.6	0.21
Friant	Friant	0	−8.4	16.1	35.0	0.21

polygons were usually sharp and clear, reflecting the flower colors of dominant taxa, the height of the vegetation, the amount of bare ground, and/or the morphology and color of leaves and stems. We located plots well away from boundaries.

For example, Fig. 2 is a diagrammatic sketch of pool No. JEP-005 from Jepson Prairie, Solano County. The pool had two visually homogenous polygons; the diagram shows where sample plots were placed in each. The deepest part of the pool (polygon A, relative elevation −15 cm) was visually distinct as bright green because of high abundance of *Lasthenia glaberrima*. There were two patches of such a polygon in this pool. Polygon B (average relative elevation −10 cm) was visually distinguished by the high abundance of the tall grass *Lolium multiflorum,* white-flowered *Limnanthes douglasii* subsp. *rosea,* and yellow-flowered *Lasthenia fremontii.* It was also different from polygon A in having much lower cover of *Lasthenia glaberrima, Eryngium vaseyi,* and *Pleuropogon californicus,* and the presence of *Blennosperma nanum* var. *nanum, Hordeum depressum, Phalaris lemonii,* and *Vulpia bromoides,* among others. Thus, polygons A and B were floristically different, both in presence or abundance of many species (Table 6). Polygon B, in the shallower part of the pool, was floristically richer, having 21 species vs. 13 for polygon A.

Our method of locating plots within polygons differs from the protocols of previous researchers. Their most common sampling design was to survey an entire pool, compiling a list of species and their abundances, thus combining in one sample species growing at the edge and the bottom. A second sampling design was to randomly or regularly place small (1 dm^2) replicate quadrats throughout the pool (e.g., Schlising and Sanders 1982; Buader 2000). In their classic summary of vegetation science, Mueller-Dombois and Ellenberg (1974, p. 46) stated that:

Regardless of the method used for field analysis, a sample . . . should fulfill the following requirements: 1. It should be large enough to contain all species belonging to the plant community; 2. The habitat should be uniform within the stand area, as far as one can determine this; and 3. The plant cover should be as homogenous as possible. For example, it should not show large openings or should not be dominated by one species in one half of the sample area and by a second species in the other half.

Neither of the sampling designs described above satisfy the requirements for classification, although they may be perfectly adequate for other objectives. Samples with size 1 dm^2 do not satisfy requirement 1, and the whole-pool sampling does not satisfy requirements 2 and 3, because pool bottoms and edges differ in their relative elevation (time of inundation) and are typically dominated by different species.

Within each polygon a 10-m^2 plot was placed. Sample plots were square when possible, but near pool edges, where polygons of homogenous vegetation were narrow, sample units usually had a rectangular shape. Typically, two or three polygons were present in a given pool, therefore an equal number of plots were taken. Because we wanted to

TABLE 3. FLORISTIC DIFFERENTIATION AMONG THE VERNAL POOL COMMUNITY TYPES. Numbers in the body of the table are constancy (percent of plots with the species present). Boldface numbers indicate species that are associated with particular community types. These species have uneven distributions that discriminate communities with high frequency of these species from those where they are absent or present with low frequency.

	Pool bottoms					Shallow pools and pool edges									Saline pools	
Community type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of plots	5	18	28	14	43	58	223	42	5	23	11	27	37	12	24	97
Eryngium vaseyi group																
Eryngium vaseyi	100	89	92	100	80	79	75	79	60	91	64	37	62	83	29	68
Plagiobothrys stipitatus var. micranthus	100	56	82	100	68	74	66	36	100	13	73	48	43	25	.	43
Lasthenia fremontii	100	67	64	36	51	83	70	81	.	87	55	59	68	8	83	81
Psilocarphus brevissimus var. brevissimus	80	72	75	43	54	69	80	52	40	70	18	19	60	.	100	88
Crassula aquatica	40	72	57	29	72	83	73	76	.	100	18	33	46	.	58	43
Deschampsia danthonioides	20	22	29	71	49	78	60	64	.	78	46	74	73	33	25	51
Callitriche marginata	80	72	21	7	35	47	43	41	.	61	18	11	62	25	13	5
Navarretia leucocephala subsp. leucocephala	.	.	79	43	33	36	36	7	.	.	64	63	.	8	.	77
Juncus bufonius	.	.	21	.	33	64	47	21	60	74	36	44	19	42	.	14
Pogogyne ziziphoroides	.	11	14	.	23	52	43	38	80	87	46	96	.	.	17	1
Eleocharis acicularis	20	.	25	14	51	53	27	5	.	44	.	.	54	8	8	18
Alopecurus saccatus	.	72	32	71	47	12	33	41	.	26	18	4	24	8	4	10
Pilularia americana	.	28	18	14	28	66	39	26	.	65	9	11	11	.	29	5
Isoetes orcuttii	20	28	14	.	30	50	33	21	80	22	27	11	22	.	.	.
Veronica peregrina subsp. xalapensis	.	17	.	.	5	.	22	17	.	22	18	7	16	.	63	30
Juncus uncialis	.	.	7	.	5	40	16	12	.	22	.	4	.	.	.	2
Juncus capitatus	.	.	4	.	12	33	15	10	.	.	.	.	3	.	.	1
Elatine californica	.	.	.	.	9	9	17	.	.	.	.	.	.	.	25	4
Lasthenia glaberrima group																
Lasthenia glaberrima	100	100	100	100	100	5	8	21	.	13	.	4	16	.	33	1
Eleocharis macrostachya	40	50	79	100	81	38	8	33	.	22	.	.	5	17	54	36
Downingia bicornuta group																
Downingia bicornuta	.	.	79	100	51	59	18	.	.	.	.	.	.	.	.	.
Ranunculus bonariensis var. trisepalus	.	.	79	.	98	48	30	.	.	.	.	.	.	17	.	.
Leontodon taraxacoides	.	.	39	.	56	91	23	2	.	.	.	.	.	.	.	.
Gratiola ebracteata	.	.	11	7	51	72	10	5	.	.	.	4	.	.	.	.
Plagiobothrys undulatus	.	17	54	14	42	5	7	2	.	.	.	.	.	.	.	.
Lilaea scilloides	.	22	4	29	42	17	7	17	.	.	.	.	.	67	.	.
Cuscuta howelliana	.	.	32	29	9	21	5	.	.	.	9	.	.	.	.	9
Downingia ornatissima	.	.	14	.	2	26	6	.	.	.	9	.	.	.	.	.

TABLE 3. CONTINUED.

Community type	Pool bottoms						Shallow pools and pool edges								Saline pools	
Community type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of plots	5	18	28	14	43	58	223	42	5	23	11	27	37	12	24	97
Hemizonia fitchii group																
Hemizonia fitchii		17			12	48	19	7	60	17	64	41	3	50	29	1
Hypochaeris glabra		6	7		14	12	39	52	100	100	18	82	35	313		
Limnanthes douglasii subsp. rosea	40	33	4				15	41	20	87	64	30	78	58		
Trifolium depauperatum			7		14	2	17	17	60	57	100	30	14	8		
Erodium botrys		28	7		28	17	40	64	60	96	18	44	11	25		
Vulpia bromoides		6	4		16	3	19	43	20	83	18	11	35		8	1
Bromus hordeaceus		6	7		7	17	34	19	100	26	36	78	41		29	5
Lepidium nitidum				14		3	5	10	80	22	18	70	46	17		
Plagiobothrys greenei	20					10	12	10	100	78	9	26				
Downingia cuspidata			4		2	22	7	5				4	19	8		
Aira caryophyllea						3	5	10		22		44		8		
Cicendia quadrangularis					14	17	25	24		74		41				
Blennosperma nanum var. nanum		6				3	5	14		57		59	51	42		
Briza minor			7		14	7	11	5		35		11				
Achyrachaena mollis group																
Achyrachaena mollis		6	4		5	5	6	17		74	100	82				6
Triphysaria eriantha subsp. eriantha							6	24		70	82	93	16	8		
Lasthenia californica						2	3	10		74	27	70	19			
Layia fremontii						14	6				82	59	14			
Microseris acuminata							0.4		40		64	74	5			
Taeniatherum caput-medusae							1	17		9	46	48				
Montia fontana group																
Montia fontana	40	4			7	2	2				9	4	70	92		
Trifolium variegatum		14			23	2	20	7	80		9		73	92		
Sidalcea calycosa	20				2		0.9						24	58		
Crypsis schoenoides group																
Crypsis schoenoides							0.9								79	55
Polypogon monspeliensis						7	2								100	56
Cotula coronopifolia		17			21		2								79	21
Plantago elongata		6			7		5	10		9	9	48	5		79	60
Downingia insignis								21							67	56
Cressa truxillensis															38	77
Myosurus minimus		17					2	7		13		4	3		42	53
Distichlis spicata		72						88		78					54	36

TABLE 3. CONTINUED.

	Pool bottoms							Shallow pools and pool edges							Saline pools	
Community type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of plots	5	18	28	14	43	58	223	42	5	23	11	27	37	12	24	97
Species with narrow distribution																
Pogogyne douglasii	**100**	.	.	.	.	.	.	.	.	.	.	.	27	.	.	.
Castilleja campestris subsp. succulenta	**20**	.	.	.	.	.	.	.	.	.	.	.	16	.	.	.
Pleuropogon californicus	.	72	43	.	.	.	5	45	.	26	.	.	.	.	.	.
Convolvulus arvensis	.	.	.	.	.	.	1	.	.	.	.	.	.	.	13	1
Isoetes howellii	.	.	.	79	9	24	5	.	.	.	.	.	3	8	.	.
Castilleja campestris subsp. campestris	.	6	4	.	12	76	6	12	.	4	.	.	.	.	.	.
Navarretia myersii subsp. myersii	.	.	.	.	.	59	.	.	.	.	.	.	.	.	.	.
Hesperevax caulescens	.	.	.	.	.	.	.	.	**100**	.	27	.	.	.	.	.
Holocarpha virgata	.	.	4	.	9	5	8	2	**100**	22	.	.	8	.	.	.
Hedypnois cretica	.	.	.	7	.	.	0.4	.	**100**	.	.	.	.	.	.	.
Mimulus tricolor	.	.	14	.	.	14	10	.	**80**	.	9	7	.	.	13	1
Medicago polymorpha	.	.	.	.	.	.	2	2	**80**	.	.	15	.	.	.	.
Trifolium gracilentum	.	.	.	.	.	.	.	.	**60**	.	.	4	.	.	.	.
Microseris elegans	.	.	.	.	.	.	.	.	**60**	.	.	.	.	.	.	.
Cerastium glomeratum	.	.	.	.	2	2	3	10	**60**	4	.	4	8	8	.	.
Psilocarphus oregonus	.	.	.	.	2	2	3	24	**80**	74	18	4	.	.	.	2
Phalaris lemmonii	.	6	.	7	.	.	0.9	17	.	83	.	4	.	.	.	.
Psilocarphus tenellus var. globiferus	.	.	4	.	.	3	11	2	.	70	.	4	8	.	4	.
Trifolium willdenowii	.	.	.	.	.	.	2	2	.	9	**91**	26	3	.	.	.
Lupinus bicolor	.	.	.	.	.	.	1	10	20	13	**64**	4	5	.	.	.
Navarretia tagetina	.	.	.	.	2	.	5	.	.	.	9	**85**	8	.	.	.
Plagiobothrys austiniae	.	.	.	.	.	.	5	.	.	.	.	**82**	14	.	.	.
Vulpia microstachys	.	6	.	.	2	.	2	2	.	.	.	**74**	30	8	.	.
Chlorogalum angustifolium	.	.	.	.	.	.	2	.	.	.	18	**67**	3	8	.	.
Plantago erecta	.	.	.	.	.	.	1	.	.	.	18	**63**	8	8	.	.
Navarretia pubescens	.	.	.	.	.	.	.	.	.	.	18	**48**	.	.	.	.
Lasthenia platycarpha	.	.	.	.	.	.	2	10	.	.	18	**44**	.	8	.	.
Minuartia californica	.	.	.	.	.	.	0.9	12	.	.	.	**41**	.	.	.	1
Linanthus parviflorus	.	.	.	.	.	.	10	.	.	.	.	**41**	.	.	.	.
Epilobium torreyi	.	.	.	.	2	.	.	.	.	.	18	**41**	5	.	4	.
Mimulus guttatus	.	.	.	.	.	.	.	.	.	.	.	.	.	**83**	.	7
Plagiobothrys glyptocarpus	.	.	.	.	.	.	.	.	.	.	.	.	8	**75**	.	.
Grindelia camporum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**80**
Epilobium densiflorum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**67**
Frankenia salina	.	.	.	.	.	.	.	.	.	4	.	.	.	.	17	**38**

TABLE 3. CONTINUED.

Community type	Pool bottoms							Shallow pools and pool edges							Saline pools	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of plots	5	18	28	14	43	58	223	42	5	23	11	27	37	12	24	97
Other species																
Hordium marinum subsp. gussonianum	.	28	25	.	58	45	70	36	100	22	64	56	70	42	38	11
Lolium multiflorum	.	56	64	21	47	36	54	79	100	91	100	52	27	92	75	2
Brodiaea sp.	.	11	7	.	12	52	39	33	60	70	100	85	62	33	.	.
Eremocarpus setigerus	.	17	46	7	33	35	29	5	80	26	55	33	16	.	4	.
Lythrum hyssopifolia	.	61	61	50	65	81	52	38	.	70	9	.	.	.	75	52
Lactuca serriola	20	11	4	.	.	.	0.9	12	60	4	.	4	3	.	.	4
Poa annua	.	.	.	.	37	5	20	2	20	13	.	7	22	58	.	.

record the complete floristic composition of the polygons, we used the biggest possible plot that would fit within the majority of polygons and be the same size for all pools and locations. By observation, plot sizes >10 m² often included visual heterogeneity, so we used plots of 10 m². A list of all taxa present, together with an estimate of each taxon's percentage cover, was recorded for each plot. Nomenclature of vascular plants follows Hickman (1993). Authorities are shown for those species mentioned in the text, which do not occur in California and in the Jepson manual (Hickman 1993).

Location data were taken for such pool traits as GPS coordinates, elevation, geomorphic surface, and soil type. Percent cover was estimated for each species present. Relative elevation below the pool edge, as a surrogate for duration time of inundation, was also noted.

Classification of community types was accomplished by placing floristic data from all sample plots into a single table. The table consisted of 356 species, subspecies and varieties (rows) × 728 plots (columns). The relative positions of rows and columns were iteratively changed so as to place together species with similar distribution among plots, and to place together plots with similar floristic composition. Technically, this was accomplished by entering habitat and vegetation data into the widely used database Turboveg, developed for storing, editing, and selecting phytosociological data (Hennekens and Schaminee 2001). Then, the numerical classification algorithm Twinspan (Hill 1979) was applied to produce a first-approximation of putative community types. These types were subsequently refined using the visual editor Megatab (Hennekens and Schaminee 2001), following the Braun-Blanquet technique as described in Westhoff and van der Maarel (1973), Mueller-Dombois and Ellenberg (1974), and Kent and Coker (1992). In order to make such a large table presentable, all plots belonging to the same community type are condensed into one column (Table 3). Each column shows the probability of species occurring within it, by their percent constancy. This sort of table, summarizing community types, is called a synoptic table.

RESULTS

Results of vernal pool vegetation classification are shown in Table 3. Each column (1–16) in this synoptic table represents a group of plots, each group differing in species composition. Thus, 728 columns have been condensed into 16 columns. Actually, Table 3 summarizes floristic data from only 667 plots; 61 plots were omitted because they did not fit within any of the 16 groups. Their removal does not necessarily mean that they were atypical or transitional; it could simply be because there were not enough replications to form them into sep-

TABLE 4. GEOGRAPHICAL DISTRIBUTION OF VERNAL POOL COMMUNITY TYPES. Numbers 1–16 along the left are the community types shown in Table 3; plus (+) indicates presence. Loc = location.

Region	Northeastern Sac. Valley Reg.						Southeastern Sac. Vall. Reg.					Southern Sierra Foothills Region							Sol-Col. Reg		
County	Tehama				Butte		Yuba	Placer	Sacramento		S-Jo	Merced				Madera	Fresno		Glen	Colu	Sola
Loc	HogL	Inks	Foor	Vina	OrovT	Book	Beal	Orch	Howd	Vale	Lane	Kels	Chan	Icord	Flyn	KenT	BigT	Fria	SNWR	Dola	Jeps
Vernal pool deep bottoms																					
1	·	·	·	·	·	·	+	+	·	+	+	·	·	·	·	·	+	·	·	·	·
2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+
3	·	·	·	·	·	·	·	+	·	+	+	·	·	·	·	·	·	·	·	·	·
4	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
5	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vernal pool shallow bottoms and edges																					
6	·	·	·	·	·	·	+	·	+	·	·	·	+	+	+	·	·	·	·	·	+
7	+	+	·	+	·	+	·	+	+	+	+	+	+	·	·	·	·	+	·	·	+
8	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·
9	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vernal pool upper edges																					
10	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+
11	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
12	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Table mountain vernal pool edges																					
13	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·
14	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Saline vernal pools																					
15	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·
16	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·

arate groups. Lines across represent species and show how each species was distributed through the 16 plot groups. Numbers within the body of the table show the percent constancy of plots within a group containing a given species. For example, *Eryngium vaseyi* was found in 75% of the 223 plots in column 7.

Each column can be called a "community type" because of the assumption that floristic similarity of plots indicates that the plots have similar ecological characteristics (Braun-Blanquet 1965). By inspection of the table and referral back to habitat information recorded for plots, it became apparent that: community types on the left portion of Table 3 are those of the wettest habitats, such as the bottoms of the deepest pools; communities in the middle are those of drier habitats, such as pool edges or within shallow pools; and the two community types on the right are those of physiologically dry, saline habitats.

All the communities along the bottom-edge-saline gradient have unique species compositions. Those species that are linked to a particular range along the environmental gradient are placed together in the table in species groups. For example, the *Eryngium vaseyi* group of species has the widest possible ecological amplitude, meaning that its species occur throughout the environmental gradient. They occur in all topographical positions, from bottoms to edges, and in all geographic locations.

Despite their similar pattern of distribution, the species of the *Eryngium vaseyi* group have different biogeographical affinities: (1) Californian vernal pool endemics (e.g., *Lasthenia fremontii, Psilocarphus brevissimus* var. *brevissimus, Navarretia leucocephala* subsp. *leucocephala, Eryngium vaseyi, Deschampsia danthonioides*); (2) more widespread wetland species with circumpolar distribution (e.g., *Eleocharis acicularis, Juncus bufonius*); and (3) introduced taxa (e.g., *Hordeum marinum* subsp. *gussonianum, Lolium multiflorum, Lythrum hyssopifolia*). Introduced taxa are placed at the bottom of Table 3 because they more typically occur in dry, non-vernal pool habitats.

In contrast, species of the *Lasthenia glaberrima* group (further down the species list) are restricted to pool bottoms, and those of the *Crypsis schoenoides* species group are limited to saline situations. Species in each group are generally listed in descending order by their constancy. Species with very low constancy and without discernible pattern distribution are not shown in Table 3.

Community types 1–5 occur in the deepest parts of vernal pools, habitats with the longest period of inundation. *Lasthenia glaberrima* was by far the more constant species within this group, often providing more than half of all plant cover. *Eleocharis macrostachya* had high presence and constancy, but contributed less cover (cover data are not shown in Table 3). The two occur throughout the Central Valley, Sierra Nevada foothills, and table mountains on

a variety of geomorphic surfaces, landforms, and soil types.

The first two community types differ between themselves in the constancy of *Pogogyne douglasii, Pleuropogon californicus,* and *Distichlis spicata.* The first community was found in vernal pool bottoms on Big Table Mountain, while the second was in slightly alkaline pool bottoms of Jepson Prairie. The next three communities (columns 3–5) differ from the first two in the added presence of species of the *Downingia bicornuta* group—*D. bicornuta, D. ornatissima, Ranunculus bonariensis* var. *trisepalus, Gratiola ebracteata, Plagiobothrys undulatus, Lilaea scilloides.* Floristically, these community types differ either in the presence of *Isoetes howellii* or in the higher constancy of species in the *Downingia bicornuta* and *Hemizonia fitchii* groups, which indicate a different length of inundation. Altogether they represent vegetation of vernal pool bottoms of the Southeastern Sacramento Valley Region in Yuba, Placer, Sacramento, and San Joaquin counties (see Table 4).

Communities 6–14 are characterized by approximately a dozen species (the *Hemizonia fitchii* species group) that occupy shallow pools or the edges of deeper pools. Presumably, these habitats are inundated for far fewer consecutive days than those of communities 1–5. Abundant populations of *Limnanthes douglasii* subsp. *rosea, Plagiobothrys greenei,* and *Blennosperma nanum* var. *nanum* are typically found at the upper edge of vernal pools where they co-exist with upland species such as the exotics *Hypochaeris glabra, Bromus hordeaceus, Erodium botrys, Vulpia bromoides, Lepidium nitidum, Aira caryophyllea,* and *Briza minor,* and the natives *Hemizonia fitchii* and *Trifolium depauperatum.* These communities occur throughout the Central Valley from low to high elevations and on different geomorphic surfaces, landforms, and soil series.

Despite their overall similarities, communities 6–14 have different habitats and species assemblages. Community type 6 has a high constancy of *Castilleja campestris* subsp. *campestris* and *Navarretia myersii* subsp. *myersii.* It was only found in two locations within the Southeastern Sacramento Valley Region on such old soil series as Corning, Redding, and San Joaquin. Community type 7 was the most commonly encountered type, recorded in >200 plots and occupying a habitat widely distributed throughout the sampled region. Community type 8 was typical of slightly saline, shallow Jepson Prairie pool bottoms and edges within the Solano-Colusa Region, and it has high constancy of *Distichlis spicata* and *Pleuropogon californicus.* Community type 9 was geographically restricted to one location in the Southern Sierra Foothills Region, and it was unique in the high constancy of *Hesperevax caulescens, Holocarpha virgata, Hedypnois cretica, Medicago polymorpha,* and *Mimulus tricolor,* among others.

TABLE 5. AFFILIATIONS OF RARE SPECIES TO COMMUNITY TYPES. Community type numbers are the same as in Table 3. Vernal pool (VP) regions are according to Keeler-Wolf et al. (1998): I—Northeastern Sacramento Valley Region; II—Southeastern Sacramento Valley Region; III—Southern Sierra Foothills Region; IV—Solano-Colusa Region. [1] FE—Federal endangered; FT—Federal threatened; SC—species of concern at the state level (CDFG Natural Diversity Data Base).

Species and their status	Number of occurrence	VP region	County	Location	Community type
Orcuttia inaequalis (FE[1])	1	III	Merced	Chance Ranch	7
Castilleja campestris subsp. *succulenta* (FT)	19	III	Fresno	Big Table Mtn.	1, 13
		III	Madera	Kennedy Table Mtn.	13, 15
		III	Merced	Chance Ranch	7
		III	Merced	Icord Ranch	7
Downingia pusilla (SC)	15	IV	Solano	Jepson Prairie	2, 7, 8, 10
		III	Merced	Kelsey Ranch	7
		III	Merced	Chance Ranch	7
Gratiola heterosepala (SC)	1	III	Fresno	Big Table Mtn.	13
Juncus leiospermus var. *leiospermus* (SC)	2	I	Butte	Oroville Table Mtn.	8, 14
Legenere limosa (SC)	8	II	Sacramento	Valensin Ranch	3, 6, 7
		II	San Joaquin	Lane Ranch	5, 7
Navarretia leucocephala subsp. *bakeri* (SC)	10	IV	Solano	Jepson Prairie	2, 8, 10

Community types 10–12 were restricted to high vernal pool edges. The presence of the upland species *Achyrachaena mollis, Triphysaria eriantha* subsp. *eriantha, Lasthenia californica, Layia fremontii, Microseris acuminata,* and *Taeniatherum caput-medusae* (the *Achyrachaena mollis* species group) characterize communities 10–12. Community type 10 was at only one location, Jepson Prairie, and it has high constancy of *Phalaris lemmonii, Psilocarphus tenellus* var. *globiferus, Distichlis spicata,* and *Psilocarphus oregonus.* Community types 11 and 12 are in the Sierran foothills of Tehama County on Red Bluff and Tuscan geomorphic surfaces, mudflows, and high terraces. Community type 11 differs in the presence of *Trifolium willdenowii* and *Lupinus bicolor.* It's distribution was restricted to Vina Plains. Community type 12 has high constancy of *Navarretia tagetina, Plagiobothrys austinae, Vulpia microstachys, Chlorogalum angustifolium,* and *Plantago erecta,* among others. This community was found on Inks Ranch and Foor Ranch.

Community types 13 and 14 represent the margins of pools on basaltic flows at 400–700 m elevation on table mountains in Butte, Madera, and Fresno Counties, situated on a Lovejoy geomorphic surface and a Hideaway soil series. They are at the highest elevation of all pool complexes we sampled. Differential species include *Montia fontana, Trifolium variegatum,* and *Sidalcea calycosa.* Community type 13 occurred on Kennedy and Big Table Mountains in the Southern Foothills Region. Community type 14 occurred on Oroville Table Mountain in the Northeastern Sacramento Valley Region and differs from 13 in the high constancy of *Mimulus guttatus, Plagiobothrys glyptocarpus,* and *Lilaea scilloides.*

Community types 15 and 16 occurred in highly saline pools of the Central Valley in Colusa and Glenn counties on Basin and Modesto geomorphic surfaces, basin and very low terrace landforms, and on Willows and Riz soil series. Characteristic species for the two communities are *Crypsis schoenoides, Polypogon monspeliensis, Cotula coronopifolia, Plantago elongata, Downingia insignis, Cressa truxillensis, Distichlis spicata,* and *Myosurus minimus* (the *Crypsis schoenoides* species group). Community type 15 was found on the Dolan Ranch, while type 16 was on the Sacramento Wildlife Reserve; the latter had high constancy of *Grindelia camporum, Epilobium densiflorum,* and *Frankenia salina.* Both communities were within the Solano-Colusa Region.

DISCUSSION

Plant communities represent within-pool vegetation mosaic. The within-pool sampling approach used in this study revealed community types that recurred from pool to pool and in some cases from one location to another. Each type was distinct in terms of its floristic composition, distribution range, and habitat features such as geomorphic surface, soil series, and relative elevation. Community types of deep and shallow parts of the same pool were floristically more different than community types that occurred in the same microhabitat but in different pools.

Table 6 summarizes the floristic composition of plots 1 and 2 from the single pool discussed in the Materials and Methods Section (Fig. 2). Bolded species in Table 6 belonged to species groups that differentiated community types in Table 3. Plots 1 and 2 shared five species with approximately similar abundances, and three other species with very different abundances. They differed, however, in

TABLE 6. FLORISTIC DIFFERENTIATION BETWEEN TWO POLYGONS WITHIN A SINGLE POOL (SEE FIG. 2). Numbers in the body of the table are species cover (%). Boldface taxa are those that defined the polygons as belonging to community types 2 or 8 in Table 3. Boldface numbers highlight species that differentiate plots 1 and 2 by their presence and/or higher abundance.

Plot number	1	2
Within pool polygon	A	B
Community type	2	8
Cover herbs (%)	75	65
Cover bare soil (%)	20	0
Cover algae (%)	5	30
Cover litter (%)	0	5
Average height herbs (cm)	20	20
Maximum height herbs (cm)	30	60
Relative elevation (cm)	−15	−12
Number of species	13	21
Common species		
Lasthenia fremontii	7	12
Eryngium vaseyi	10	3
Pleuropogon californicus	10	4
Distichlis spicata	0.5	3
Lythrum hyssopifolia	0.5	0.1
Differential species		
Lasthenia glaberrima	**50**	1
Plagiobothrys stipitatus var. micranthus	**1**	.
Alopecurus saccatus	**0.5**	.
Eleocharis macrostachya	**0.1**	.
Psilocarphus brevissimus var. brevissimus	**0.1**	.
Cotula coronopifolia	**0.1**	.
Lolium multiflorum	0.5	25
Limnanthes douglasii subsp. *rosea*	0.1	**10**
Blennosperma nanum var. *nanum*	.	**2**
Vulpia bromoides	.	**1**
Pogogyne ziziphoroides	.	1
Hordeum depressum	.	1
Phalaris lemmonii	.	1
Trifolium depauperatum	.	**0.5**
Trifolium barbigerum	.	0.5
Lactuca serriola	.	0.5
Hemizonia fitchii	.	**0.1**
Erodium botrys	.	**0.1**
Cerastium glomeratum	.	0.1
Crassula aquatica	.	0.1
Hordeum marinum subsp. gussonianum	.	0.1

the presence/absence of 18 species. The analysis of all 728 plots placed plots 1 and 2 into community types 2 and 8, respectively. Community type 2 was found in 18 plots from 10 pools, and community type 8 in 42 plots from 19 pools. That is, plot 1 was floristically more similar to 17 plots that occurred in other pools than it was to adjacent plot 2. Communities 2 and 8 were often found together in the same pool, but sometimes only one of them, either alone or in combination with a community of some other type. Thus, plant communities within a pool are more or less autonomous; that is, they

can develop separately from each other in different vernal pools.

The sampling approach that uses many replicates 1 dm^2 plots addresses patterns of individual species distributions (Schlising and Sanders 1982; Buader 2000). At the other extreme, the sampling approach that uses whole-pool data combines vegetation of all habitats occurring in a single pool in one sample. This latter approach is focused on vegetation complexes and their connections with geologic formations, soils, or geographical distribution (Holland 1976; Sawyer and Keeler-Wolf 1995; Fiedler and Ferren 1999). Our sampling technique, based on 10 m^2 plots, uses an intermediate plot size between the two approaches described above. It captures another vernal pool attribute—the plant communities, which may be identified by repeatable species assemblages. The communities represent an intermediate phenomenon between individual species distribution and whole-pool vegetation complexes, and they are more similar to community types as accepted in the European tradition (Braun-Blanquet 1965; Westhoff and Maarel 1973; Mueller-Dombois and Ellenberg 1974).

Plant communities are geographically autonomous. The previous section described the topographic autonomy of within-pool plant communities. These communities also exhibit geographic autonomy. That is, the same community type was encountered in several locations within the same vernal pool region or sometimes even in different regions. Most community types were local, restricted to a few locations within a single region or even to a single location in a single region. Community type 7 was exceptional in being found in all four vernal pool regions (Table 4). Each location and each vernal pool region differed in the number of community types encountered. Jepson Prairie pools, for example, had four community types, one deep pool type and three edge or shallow pool types. This community richness may be a consequence of the complex topography at Jepson, where the pools are large and interconnected by swales. Howard Ranch pools had three community types, one deep pool and two edge types. Big Table Mountain pools had two community types, one in deep pools and one at the edge. Foor Ranch pools, in contrast, were shallow and small, well-constrained by intervening mima mounds, and they were comprised of a single community type (Table 4). The implications of these patterns for conservation are profound: conservation and mitigation measures must be locally focused.

As most of our community types are restricted to a single vernal pool region defined by Keeler-Wolf et al. (1998) our results largely correspond with classifications that have been developed based on a whole-pool approach (Holland 1976; Sawyer and Keeler-Wolf 1995; Keeler-Wolf et al. 1998).

TABLE 7. ASSOCIATION *Downingio bicornutae-Lasthenietum fremontii ass. nova.* Releve 1 is the nomenclatural type of the association; data are percent cover. All releves are among the 223 releves that appear in column 7 of Table 3.

Plot number	1	2	3	4	5	6	7	8	9	10	11	12
Field number	11C	20A	20B	20D	30A	31A	40B	40C	40D	60A	62A	1B
Area (sq. m)	10	4	6	10	10	10	10	10	10	10	10	10
Relative elevation (cm)	−8	−8	−6	−4	−17	−19	−4	−1	.	−8	−19	−9
Cover herb layer (%)	80	85	80	80	80	85	70	65	60	85	75	65
Cover soil (%)	20	15	20	20	15	15	30	35	40	15	25	35
Cover litter layer (%)	10	5	1	10	30	60	35	5	5	10	5	5
Aver. height (high) herbs (cm)	10	12	5	10	15	20	10	8	12	15	10	10
Maximum height herbs (cm)	30	35	25	35	45	40	25	25	35	35	35	20
Cover punch (%)	5	1	10	20	15	1	0	2	1	1	5	5
Number of species	15	20	22	15	19	23	20	24	23	20	19	23
Diagnostic species of association *Downingio bicornutae-Lasthenietum fremontii*												
Lasthenia fremontii	17	28	5	16	25	35	25	10	20	15	18	8
Downingia bicornuta	2	2	1	2	.	2	.	1	1	.	.	0.5
Downingia ornatissima	.	.	.	.	5	2	2	1	1	0.5	3	.
Diagnostic species of class *Downingio bicornutae-Lasthenietea fremontii*												
Eryngium vaseyi	8	3	3	4	7	2	3	10	7	2	5	2
Deschampsia danthonioides	17	13	5	16	30	35	30	1	7	0.5	0.5	0.5
Navarretia leucocephala subsp. *leucocephala*	17	4	18	21	2	1	5	5	1	1	1	2
Crassula aquatica	.	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Pogogyne ziziphoroides	0.5	1	.	.	.	0.5	0.5	1	0.5	1	1	0.5
Juncus bufonius	.	.	.	.	.	.	0.5	0.5	0.1	0.5	0.5	0.5
Plagiobothrys stipitatus var. *micranthus*	.	0.5	0.5	1	0.5	0.5	0.5	.	.	.	.	1
Psilocarphus brevissimus var. *brevissimus*	.	2	1	.	0.5	0.5	.	.	0.5	0.5	.	1
Pilularia americana	.	0.1	0.5	.	.	.	.	0.5	.	.	.	.
Isoetes orcuttii	.	0.5	.	.	.	.	.	.	.	.	.	.
Callitriche marginata	0.5	.	0.1	.	.	.	.	.	.	0.5	.	3
Juncus uncialis	.	.	0.5	0.5	.	.	.	.	.	.	.	.
Alopecurus saccatus	.	.	.	.	.	.	.	0.5	.	.	.	.
Elatine californica	.	.	.	.	.	.	.	.	0.5	.	.	.
Eleocharis acicularis var. *acicularis*	.	.	.	.	.	.	.	.	.	.	.	0.5
Diagnostic species of order *Downingio-Lasthenietalia* and alliance *Downingio-Lasthenion*												
Hemizonia fitchii	0.5	.	0.5	2	0.5	1	0.5	0.5	0.5	7	2	2
Castilleja campestris	0.1	0.1	1	2	1	0.5	.	0.5	0.5	0.5	.	.
Gratiola ebracteata	0.1	0.5	.	1	1	0.5	2	1	0.5	.	0.5	.
Ranunculus bonariensis var. *trisepalus*	0.5	0.5	.	.	0.5	0.5	0.5	0.5	.	2	0.5	3
Cuscuta howelliana	.	2	1	1	3	0.5	.	.	15	.	.	0.1
Plagiobothrys undulatus	.	.	.	.	.	.	.	1	.	.	.	.

TABLE 7. CONTINUED.

Plot number	1	2	3	4	5	6	7	8	9	10	11	12
Field number	11C	20A	20B	20D	30A	31A	40B	40C	40D	60A	62A	1B
Other native species												
Eleocharis macrostachya	·	4	2	·	·	·	0.5	1	0.5	0.5	0.5	0.5
Eremocarpus setigerus	0.5	·	0.5	·	·	0.5	3	1	0.5	0.5	0.5	0.5
Trichostema lanceolatum	0.5	·	1	·	3	5	1	·	1	·	0.1	·
Centunculus minimus	·	0.5	·	·	·	0.5	0.5	0.5	0.5	0.5	·	0.1
Callitriche heterophylla	0.5	·	·	·	·	·	·	·	0.5	·	·	·
Achyrachaena mollis	0.5	·	1	·	·	·	·	·	·	·	·	·
Allium amplectens	·	·	·	1	·	·	·	·	·	·	·	·
Epilobium sp.	·	·	·	·	·	·	·	·	·	·	·	·
Polygonum arenastrum	·	·	·	·	0.1	·	·	·	·	·	·	·
Lasthenia glaberrima	·	·	·	·	·	·	0.5	·	·	·	·	·
Brodiaea sp.	·	·	·	·	·	·	·	0.5	·	·	·	·
Invasive species												
Leontodon taraxacoides	0.5	10	32	10	1	0.5	0.5	1	3	25	25	40
Lythrum hyssopifolia	0.5	0.5	0.5	0.5	0.1	0.5	0.5	1	0.5	0.5	1	0.5
Hordeum marinum subsp. gussonianum	·	1	·	·	0.5	2	·	20	·	30	·	1
Lolium multiflorum	8	·	·	·	0.5	·	·	7	0.5	1	15	·
Glyceria declinata	·	·	·	·	·	0.5	0.5	0.5	·	·	·	·
Polypogon monspeliensis	·	·	·	·	·	1	·	·	·	0.5	·	·
Juncus capitatus	·	·	0.5	·	·	·	·	·	·	·	·	1
Hypochaeris glabra	·	·	·	·	·	·	·	·	0.5	·	·	0.1
Erodium botrys	·	·	·	·	·	·	·	·	·	·	0.5	·

Plant communities and rare species. Seven rare and threatened species of vascular plants were found on our sample plots and are affiliated with particular community types, vernal pool regions, counties, and locations (Table 5). Some rare species have a broader distribution then others. *Orcuttia inaequalis* (federal endangered species) has a narrow ecological range and geographical distribution. This species was encountered only in one community type (7) on Chance Ranch. *Gratiola heterosepala* was also restricted to one community type (13) and in one location (Big Table Mountain). *Castilleja campestris* subsp. *succulenta* was encountered in four community types (1, 7, 13, 15) at four different locations, all restricted to the Southern Sierra Foothills vernal pool region (Table 5). *Downingia pusilla* grew in four community types (2, 7, 8, 10) in Jepson Prairie, Kelsey, and Chance Ranches in Solano-Colusa and Southern Sierra Foothills vernal pool regions. In Jepson Prairie alone, *D. pusilla* occurred in all four community types, while at Kelsey and Chance Ranches it was restricted to community type 7. *Juncus leiospermus* var. *leiospermus* has been found both in the bottoms (type 8) and edges (type 14) of vernal pools on Oroville Table Mountain. *Legenere limosa* grew in both deep (types 3, 5) and shallow bottoms (types 6, 7) in Valensen and Lane Ranches within the Southeastern Sacramento Valley vernal pool region. *Navarretia leucocephala* subsp. *bakeri* was found in community types 2, 8, and 10 at Jepson Prairie.

Some community types supported several rare species, while others had only one or none (Table 5). For example, community type 7 supported four different rare species, while community type 13 supported two species. Rare species were not found in community types 4, 9, 11, 12, and 16. The presence of rare species will contribute to the conservation value of a given community type, and the relationship between community type and the presence of a rare species will be helpful in the search for new locations of the species.

Syntaxonomical interpretation of Californian vernal pool vegetation. The within-pool sampling approach is compatible with classification approaches of European ephemeral wetlands, and are assigned to the class *Isoeto-Nanojuncetea* Br.-Bl. et Tx. ex Westhoff, Dijk et Passchier 1946. This class unites pioneer, ephemeral, dwarf cyperaceous, and therophyte plant communities on bare, periodically flooded ground (Pietsch 1973; Philippi 1977; Deil et al. 1999). Presence of *Limosella aquatica, Juncus bufonius, J. capitatus, Androsace filiformis, Gnaphalium uliginosum* L., *Gypsophila muralis* Gypsy., *Cyperus fuscus, Plantago major* L. subsp. *intermedia (DC.), Riccia bifurca Hoffm.,* and other ephemeral semi-aquatic species indicates the habitat conditions, differentiating this class from other European vegetation types.

Californian vernal pools are similar to European communities of the class *Isoeto-Nanojuncetea* in the joint presence of *Centunculus minimus, Crassula aquatica, Eleocharis acicularis, Juncus bufonius, J. capitatus, Lythrum hyssopifolia, Mentha pulegium, Montia fontana,* and *Myosurus minimus.* They are also similar at the generic level, sharing vicariant species of *Callitriche, Elatine, Eleocharis, Isoetes, Marsilea,* and *Pililaria.* At the same time, Californian vernal pools are uniquely characterized by the high number of genera endemic to California or the west coast of North and South America, such as *Downingia, Lasthenia, Navarretia, Plagiobothrys, Pogogyne, Psilocarpus.* These endemic taxa also typically contribute high cover. Thus, Californian and European ephemeral wetlands represent vicariant, but floristically very distinctive, vegetation types.

We recognize Californian vernal pool vegetation as a new class, *Downingio bicornutae-Lasthenietea fremontii class nov. hoc loco.* This class represents all types of Great Central Valley vernal pool vegetation occurring on all geomorphic surfaces, landforms, and soil types. The class includes plant communities of hardpan, claypan and volcanic vernal pools as described by Holland (1976, 1978), including those on fresh or alkaline soils and those in deep or shallow pools. Diagnostic species of the class (in decreasing constancy, as in Table 3) are: *Alopecurus saccatus, Callitriche marginata, Crassula aquatica, Deschampsia danthonioides, Elatine californica, Eleocharis acicularis, Eryngium vaseyi, Isoetes orcuttii, Juncus bufonius, J. uncialis, Lasthenia fremontii, Navarretia leucocephala, Pilularia americana, Plagiobothrys stipitatus* var. *micranthus, Pogogyne ziziphoroides, Psilocarpus brevissimus* var. *brevissimus, Veronica peregrina* subsp. *xalapensis.* The nomenclatural type of the class (*holotypus*) is the order *Downingio bicornutae-Lasthenietalia fremontii ord. nov. hoc loco.*

Diagnostic species of the order *Downingio bicornutae-Lasthenietalia fremontii ord. nov. hoc loco.* are *Blennosperma nanum* var. *nanum, Cicendia quadrangularis, Downingia cuspidata, Hemizonia fitchii, Lepidium nitidum, Limnanthes douglasii* subsp. *rosea, Plagiobothrys greenei, Trifolium depauperatum* var. *depauperatum.* The nomenclatural type of the order (*holotypus*) is the alliance *Downingio bicornutae-Lasthenion fremontii all. nov. hoc loco.*

Diagnostic species for the alliance *Downingio bicornutae-Lasthenion fremontii all. nov. hoc loco.* are *Castilleja campestris, Cuscuta howelliana, Downingia bicornuta, D. ornatissima, Gratiola ebracteata, Lilaea scilloides, Plagiobothrys undulatus, Ranunculus bonariensis* var. *trisepalus.* The nomenclatural type of the alliance (*holotypus*) is the association *Downingio bicornutae-Lasthenietum fremontii ass. nova hoc loco.* The order and alliance unite vegetation of comparatively shallow vernal pool bottoms and edges. Floristic diversity is rather high, because species from surrounding grasslands

(e.g., *Hemizonia fitchii, Hypochaeris glabra, Bromus hordeaceus, Briza minor, Brodiaea spp., Eremocarpus setigerus* etc.) usually co-occur with typical vernal pool species.

Diagnostic species of the association *Downingio bicornutae-Lasthenietum fremontii* ass. nova hoc loco are *Lasthenia fremontii, Dowingia bicornuta,* and *D. osnatissima.* The nomenclatutal type of the association (*holotypus*) is the releve No. 1 in Table 7 (taken 4 May 2001, field number BEA11C, author—R. Holland). The association comprises plant communities of vernal pools on the San Joaquin soil series, low terrace landform, and Riverbank geomorphic surface. The releves were taken at Beale Air Force Base in the Yuba County located to the north of Sacramento. The communities develop in comparatively shallow locations, from the edge down to -19 cm below the edge, with and average depth of -9 cm. Soils are presumably non-saline, because no species indicating salinity or alkalinity were found. Communities of the association are typically dominated by *Lasthenia fremontii, Navarretia leucocephala* subsp. *leucocephala, Eryngium vaseyi,* and *Deschampsia danthonioides.* The widespread vernal pool species *Crassula aquatica, Pogogyne ziziphoroides, Juncus bufonius, Gratiola ebracteata, Ranunculus bonariensis* var. *trisepalus,* among others, are typically present with high constancy, but with low cover. The invasive species *Leontodon taraxacoides, Lythrum hyssopifolia, Hordeum marinum* subsp. *gussonianum,* and *Lolium multiflorum* are common. *Leontodon taraxacoides* often is abundant. Total herb cover varies from 65 to 85%. Average height of herbs is 11 cm. The number of species per 10 m^2 varies from 15 to 24, with an average of 20.

We followed the International Code of Phytosociological Nomenclature (Weber et al. 2000) in naming the association, alliance, order, and class.

Conclusions

The vegetation of a whole pool thus represents a complex of several apparently independent communities, each of which can be found in other pools, and may have individual geographical distribution. This fundamental characteristic of vernal pool vegetation could not have been revealed, had we sampled according to the whole-pool model, traditionally used for classification of California vernal pools.

The fact that whole vernal pools typically do not represent one floristically homogenous vegetation type, but instead consist of a complex of plant communities, changes our perception of vernal pool vegetation. The distribution of community types was not random, but depended upon geographical and environmental factors. Further research may determine the "assembly rules" (Weiher and Keddy 1999) that restrict the number and variety of possible combinations of species and community types within pools. Such knowledge will extend our understanding of vernal pool vegetation, and will clarify restoration and conservation objectives. This is the first paper from an on-going multi-year project, and it has focused on the within-pool approach. Only data from northern California were included. Future publications will deal with ecofloristic classification throughout California.

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FLORISTIC ANALYSIS OF AN INTERIOR VERNAL POND COMPLEX, SANTA BARBARA COUNTY, CALIFORNIA

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ABSTRACT

In Santa Barbara County, research and restoration on vernal wetlands has historically concentrated on coastal areas. Emerging conservation issues have highlighted the need for more information about the floristic composition of vernal wetlands in the interior region of the County. This paper provides data on the vegetation of the Long Canyon vernal pond complex on the University of California's Sedgwick Reserve collected during the El Niño-dominated winter and spring of 1997–1998. A multivariate vegetation analysis was used to compare the site's species composition with other localities in the region. The analysis was supplemented by a simulation-based error analysis evaluating the potential impacts of species omission on Sorensen similarity distances. Floristically, the Sedgwick Reserve vernal ponds were expected to align most closely with nearby vernal pools in Northern Santa Barbara County. However, the results do not support this hypothesis; rather, the wetlands are most similar to coastal vernal pools along the south coast of Santa Barbara County.

Key Words: Vernal wetlands, Sedgwick Reserve, biogeography, floristic composition, error analysis.

Vernal pools and ponds are shallow, temporary wetlands formed by the accumulation of water from winter rains on impermeable substrates (Holland and Jain 1981; Weitkamp et al. 1996; Bauder et al. 1997). These ephemeral wetlands are among the most imperiled wetland types in California (Holland and Jain 1981; Ferren and Pritchett 1988; Ferren and Gevirtz 1990; Stone 1990; Rietner 1996; Bauder et al. 1997), and approximately 90% of the vernal pools in southern California have been destroyed in the past century (Ferren and Pritchett 1988). Not surprisingly, this trend is putting a growing number of species at risk of extinction. The majority of vernal pool research in Santa Barbara County has focused on coastal areas (Ferren and Pritchett 1988; Ferren and Gevirtz 1990). However, the geographic distribution and floristic characteristics of interior vernal wetlands are not well known, and conservation efforts require additional information for the identification, classification, and preservation of interior vernal wetlands (U.S. Fish and Wildlife Service 2000).

This paper provides preliminary information about the physical environment and floristic composition of an interior vernal wetland complex in the valley-foothill region of Santa Barbara County. The vernal ponds studied in this project may be representative of a significant number of poorly known vernal wetlands, the majority of which occur on inaccessible private lands. The study took advantage of exceptionally wet conditions following the El Nino-dominated winter of 1997–1998 to characterize the vernal ponds near the peak of inundation and duration and compare their floristic composition to other vernal wetland localities in southern California.

Vernal Wetland Biogeography and Classification

Vernal pools and ponds are members of the class of depressional wetlands in the widely used hydrogeomorphic classification model (Brinson 1993). In coastal areas, vernal wetlands occur as seeps, swales, pools, or ponds in areas of low relief, typically along coastal terraces or mesas (Norwick 1991). In some cases, their distribution may be controlled by geological structures such as joints or faulting (Ferren et al. 1995). Vernal wetlands in interior areas are more poorly defined, but observations suggest that they can occur in a variety of geomorphological settings. Known locations include ridge tops (e.g., a single vernal pond on Sulfur Mountain in Ventura County), abandoned river terraces (e.g., Orcutt and Cachuma Canyon), or valley bottoms (e.g., Sedgwick Reserve). The classification and description of vernal wetlands is currently the subject of research, and possibly revision, across California (Ellen Bauder personal communication). This paper follows the conventions presented by Ferren et al. (1995) for wetlands of central California coast.

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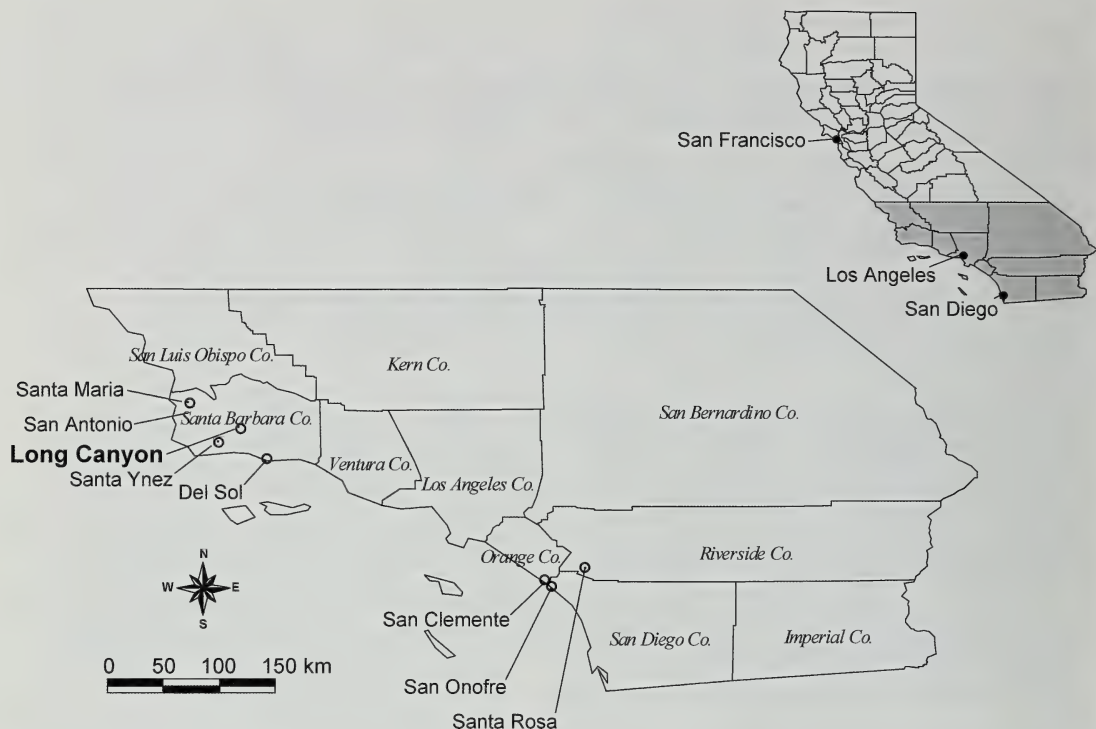
Fig. 1.   Location of the Long Canyon study area (bold text) and other vernal wetland localities used in this study (marked with circles). Note that both Surf Beach and the Trestles Unit are part of San Onofre State Beach (north of San Diego).

Hydroperiod defines the amount of time that surface water is present in a vernal wetland. Field studies from the Central Valley of California suggest that vernal pools fill almost exclusively from the direct interception of rain water (Hanes and Stromberg 1998). Vernal ponds have longer hydroperiods, and they may receive supplemental water from surface runoff or groundwater (Ferren et al. 1995). Anecdotal evidence suggests that both types of wetlands have high inter-annual variability in flooding onset, the maximum depth of inundation, and the seasonal duration of inundation (Bliss and Zedler 1998). During years with low precipitation, vernal wetlands may remain dry, while an average year may be characterized by several cycles of filling and drying. High-precipitation conditions can produce large wetlands, longer periods of inundation, and variation in observed flora and fauna. Vernal wetland vegetation has been observed to oscillate between invasion by upland species during drought periods and reestablishment and dominance of wetland species during wetter conditions (Ferren and Pritchett 1988; Ferren and Gevirtz 1990). Consequently, we hope the El Niño conditions during this study provided the opportunity to observe a relative abundance of wetland species.

Study Site

The investigation focused on a vernal pond complex in Long Canyon on the University of California's Sedgwick Reserve in Santa Barbara County (Fig. 1). Sedgwick Reserve is part of a statewide set of managed lands controlled by the University of California Natural Reserve System. The 2,500-hectare ranch was used historically for agriculture, including extensive cattle ranching and forage-crop production, and the reserve is currently managed as an experimental field station for research in ecology, soil science, and rangeland management. The vernal wetlands described in this study occur at an elevation of approximately 275 m on the Paso Robles alluvium.

The Long Canyon wetland complex is located in the southwestern corner of the reserve, and it consists of two vernal ponds separated by approximately 50 m. The southern (down-valley) pond in the Long Canyon complex is approximately 10 m long and 30 m wide, and it has been classified as palustrine emergent-persistent (*Eleocharis*) seasonally flooded vernal-marsh wetland (Fig. 2). The northern pool is smaller, approximately 6 m by 25 m, and it has been described as a palustrine unconsolidated-bottom (mud) seasonally flooded vernal-

Fig. 2.   Photograph looking north up Long Canyon from the upper vernal pond on Sedgwick Reserve. *Eleocharis macrostachya* dominates the emergent vegetation in the foreground.

pond wetland (Ferren et al. 1995) (Fig. 2). They are connected during wet years by drainage along an abandoned dirt road extending the length of the canyon. The ponds are surrounded by naturalized grassland in a valley flanked by stands of *Quercus agrifolia* (coast live oak) and *Quercus douglassii* (blue oak). Scattered *Quercus lobata* (valley oaks) occur on the canyon bottom as it widens to the east. The south-facing exposures on Long Canyon are dominated by coastal sage scrub.

Several prominent landslide scars mark the slopes above the wetlands. Most of the slides appear to originate in areas of sage scrub and deposit debris on the grassy areas below. Side valleys also channel sediments to the valley floor, frequently forming lobes of debris. A combination of landslides and channeled debris flows appear to have created an alluvial dam below the ponds. We hypothesize that the dam impounded runoff and resulted in the accumulation of fine sediments as water was forced to infiltrate beneath the slide deposits. The resulting clay pan is dark brown to black in color, extremely plastic, at least 25 cm thick, and it appears to sharply delimit the extent of the ponds. Its maximum thickness is unknown because digging deeper than 35 cm was impossible without damage to wetland vegetation. The ponds seem to be sharply delimited by the presence of underlying clay lenses. Beyond the margin of the wetland vegetation, soils return quickly to the coarse gravel. The *Northern Santa Barbara County Soil Survey*

(Shipman 1981) describes these valley bottom soils as part of the Salinas series; however, it is important to note that that clay layers are probably controlled by local geomorphology rather than in situ pedogenesis.

Up valley from the wetlands, a spring feeds water into the ponds through a large wet-meadow wetland. Alluvial valleys with Paso Robles sediments are often known to have significant amounts of near-surface groundwater flow with large seasonal variations in depth to the water table. Test wells in nearby Lisque Creek show that the groundwater table varies between 0 and >10 m below the surface (Oliver Chadwick personal communication). Given the similar geology and geomorphic settings, we believe that a similar mechanism conveys water down Long Canyon, and groundwater probably provides a significant supplement to the direct interception of rainwater on the impermeable pond basins.

Hydrology and Climate

The 1997–1998 rainfall year was characterized by exceptional rainfall accumulations associated with an unusually strong El Niño event in the Pacific Ocean. Cumulative rainfall for the first part of 1998 (January 1 to April 19) was approximately five times greater than during the same period during the winter of 1997. The ponds began to fill in mid-January, and they were well developed follow-

TABLE 1. On-site Climatic Information Is Unavailable for Most of the Wetlands in this Comparison. Data for the closest available meteorological station appear below. Source: Western Regional Climate Center (http://www.wrcc.dri.edu/). [1] Riverside Fire Station #3, [2] Santa Barbara Airport, [3] Laguna Beach (these values apply to the wetlands at Surf Beach and the Trestles Unit), [4] Oceanside Marina, [5] Sedgwick Ranch meteorological station (UCSB Pedology Group), [6] Santa Maria Airport.

	Santa Rosa[1]	San Clemente[4]	San Onofre[3]	Santa Maria[6]	Long Canyon[5]	Del Sol[2]
Avg. max./min	26.4	20.2	21.7	20.4	24.9	20.8
temp (°C)	9.4	11.7	10.5	7.7	7.4	9.3
Mean annual ppt. (cm)	27	27	33	33	38	40
Elev. (m)	256	18	12	73	259	3

ing a series of intense rainstorms during February (cumulative 41 cm, 1/25/1997–2/23/1998, average annual precipitation 38 cm). Small areas within each pond basin remained flooded after the end of our floristic fieldwork in June 1998. Subsequent observations indicate that the ponds dried completely during early July 1998. This suggests a flood duration of 6–7 months, which exceeds Bauder et al.'s (1997) observations that southern California vernal pools typically remained flooded 3–5 months per year.

METHODS

We began our investigation of the vernal ponds on April 25, 1998 by creating a rectangular sampling grid at each pond. The primary axis for the grid was established in a north-south direction parallel to the long axis of the wetlands. This transect skirted the east side of the ponds and included all wetland species along the pond margin. We then established sampling transects in an east-to-west direction across the ponds at 10-m intervals perpendicular to the primary axis. Our initial data collection included water-depth measurements taken along each transect at 2-m intervals. Pool size and depth were sampled weekly at 2-m intervals along each transect line until the ponds diminished to the point that they no longer intercepted the stations (after 6/7/1998).

We conducted extensive plant surveys on two dates: April 25 and May 17, 1998. The first session totaled 3 person-hours of searching while the second totaled 1.75 person-hours of effort. We looked less intensively for additional species during each weekly water monitoring visit. Botanical surveys consisted of walking pond-perimeter transects in a clockwise direction, and they were limited to the vegetated edge surrounding the open-water ponds and 2 m into adjacent upland areas. Samples of all plant species observed growing in this area were collected and identified based on *The Jepson Manual* (Hickman 1993) and the *Checklist of Vascular Plants of Sedgwick Reserve* (Thomas et al. 1996). All species names in Appendix 1 follow Hickman (1993). Specimens were also collected and identified with reference to material at the University of California at Santa Barbara Museum of Systematics and Ecology Herbarium.

We compared the floristic composition of the Sedgwick Ranch vernal ponds complex with other well-documented vernal wetlands in southern California. Data from other sites was compiled from the best available information in peer-reviewed (Lanthrop and Thorne 1976; Rietner 1996) and "gray" literature sources (Ferren and Pritchett 1988; Olson 1992) (Appendix 1). The sites range in elevation from 3 m (Del Sol Preserve) to 259 m (Sedgwick Reserve) and in mean annual precipitation from 26.7 cm/year (San Clemente) to 40.4 cm/year (Del Sol Preserve) (Table 1). Collection and inventory efforts and methods vary by site and readers are referred to the original publications for details. The Del Sol vernal pools are probably the most extensively degraded, and they have been extensively restored since the early 1980's (Ferren and Pritchett 1988). Species richness varied between 17 species for the San Antonio area of Northern Santa Barbara County (Olson 1992) to 101 species for San Clemente State Beach (Rietner 1996); however, these totals probably reflect more variation in methods than variability in floristics, as workers appear to have included varying percentages of upland species in their totals (94% wetland species at San Antonio, 55% at San Clemente State Beach). We accommodated these differences by using USFWS definitions to separate plants with obligate and facultative wetlands relationships from non-indicators and upland species. Cluster analysis was performed for both sets of plants separately.

The PC-ORD (version 4.0) software package was used for an agglomerative, hierarchical cluster analysis for 10 vernal wetland localities (McCune and Mefford 1999). The Sorensen distance measure with farthest neighbor group linkage was used to construct the dendrogram presented in Fig. 2. The Sorensen distance measure is a standard vegetation analysis method (McCune and Mefford 1999), and it provides an index of similarity between samples—in this case, vernal pool complexes based on the presence or absence of partially overlapping sets of species. Wetlands sharing 100% of their species would have a Sorensen score of 1.00. We se-

TABLE 2. FLORISTIC COMPARISON OF TEN VERNAL POOL LOCALITIES ACROSS SOUTHERN CALIFORNIA.

	Number of species	Number of genera	Number of families	Percent native	Percent wetland	Percent wetland obligate
Santa Barbara (San Antonio)	17	16	13	82	94	35
Santa Barbara (Santa Maria)	28	22	14	82	82	43
Santa Rosa Plateau	30	20	18	97	90	57
Del Sol restored pools	45	36	16	47	76	11
Del Sol natural pools	48	38	19	50	77	13
Santa Barbara (Santa Ynez)	48	42	22	67	77	21
San Onofre (Trestles)	49	39	20	47	61	12
Sedgwick vernal ponds	61	49	21	46	72	10
San Onofre (Surf Beach)	73	60	27	38	63	10
San Clemente State Beach	101	76	28	50	55	3

lected the Sorensen index for this analysis because it emphasizes the joint occurrence of species, rather than their mutual absence, in determining a coefficient of similarity. This quality is an advantage for vernal wetlands where we are confident of the occurrence of species discovered by our inventories, but relatively unsure of species absences without long-term monitoring.

Given the limited time available for plant collection and the rapid changes in phenology characteristic of vernal wetlands, we may have missed species through error, oversight, or simple chance. We performed a quantitative analysis to evaluate the implications of the addition of potentially missed species from our list at Sedgwick for calculations of floristic distance between localities. This simple, but we believe novel procedure, assumes that the most likely error was one of omission, and that the omitted species are also found elsewhere and are listed in the combined set of species from all sites (i.e., omitted species are not endemic to Sedgwick Reserve). Essentially, the test evaluated the sensitivity of our observations to the addition of a given percentage of the species that might have been found in a "complete" survey. We wrote a Visual Basic computer program to randomly select a given percentage of potentially omitted species from the combined species list, create a new, "Sedgwick Error" locality by combining the additional randomly selected species with the observed Sedgwick species list, and then recalculate the Sorenson similarity distance between the "Sedgwick Error" locality and all other sites. This resampling was performed 100 times for each of six error levels (61 species + 5%, 10%, 20%, 30%, 40%, and 50%), and the Sorensen distances between Sedgwick Error and each site were averaged (n = 100). The distance between Sedgwick Error and itself is always zero (100% similarity), and the distance from the observed Sedgwick list varies directly with the level of error simulated (i.e., greater percentages of species added equate to higher Sorensen distances). Changes in the Sorensen distance between Sedgwick Error and other sites reflect the chance that the addition of species to the Sedgwick list would

reduce the dissimilarity between the two localities by adding another common species. Errors in species identification or omissions at other localities were not considered.

RESULTS

At the time of our survey, the margins of the wetlands were dominated by perennial *Eleocharis macrostachya* and several varieties of annual *Hordeum* spp. The ponds reached peak areas of approximately 80 m² (upper pond) and 110 m² (lower pond), and maximum depths of approximately 40 cm (upper pond) and 50 cm (lower pond) (Fig. 3). Overall, we observed 61 species in 49 genera (Appendix 1). A large fraction of the plants consisted of facultative wetland species (72%) with only a small percentage of wetland obligates (10%). In comparison to other vernal wetlands, the site had a relatively low percentage of native species at 46%. These statistics compare to the 12-site average species richness of 52 (s.d. = 22), 75% (s.d. = 11) facultative species, 21% (s.d. = 16) obligate species, and 60% (s.d. = 19) native for the entire group (Table 2). Tests of statistical significance were not performed due to the small sample size. The wet-meadow grasslands up-valley of the ponds also contained a small fraction of wetland vegetation primarily, *E. macrostachya,* dominated by upland vegetation including *Bromus, Hordeum,* and *Lolium* spp. The ponds and wet meadow supported dense populations of western spade-foot toads (*Scaphiopus hammondi*) and Pacific tree frogs (*Hyla regilla*).

The cluster analysis yielded two dendrograms, one for all species (Fig. 4) and a second for only obligate and facultative wetlands species (Fig. 5). Both dendrograms indicate that the Sedgwick wetland complex is most similar to both the natural and restored vernal pools of the Del Sol Preserve. The Sedgwick wetlands are least similar to the Santa Rosa vernal pools. The major divisions in the dendrogram follow broad geographic areas, in order of decreasing similarity from Sedgwick: Del Sol (coastal), San Onofre (coastal), San Clemente

Upper Pool Perimeter
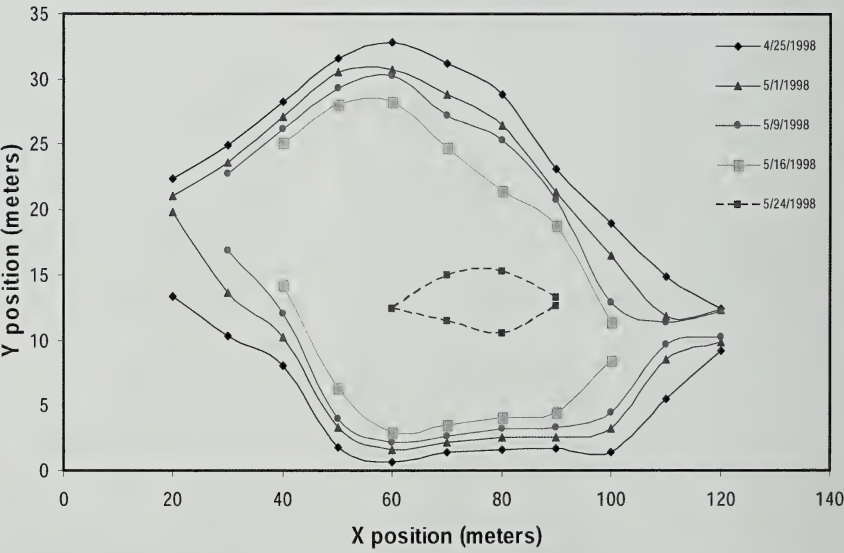

(a)
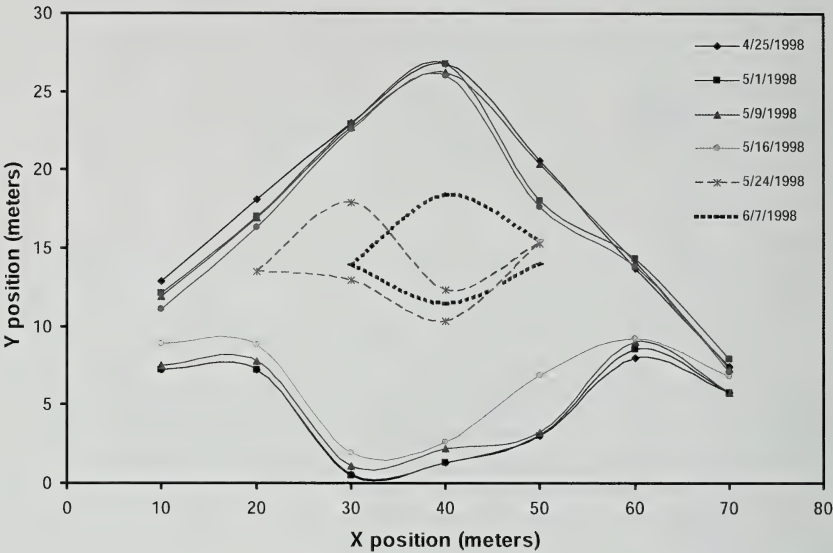
Lower Pool Perimeter

(b)

Fig. 3. Plots of pool surface area as a function of date of observation between its peak on 4/25/1998 and the last flooded sampling date on 6/7/1998.

(coastal), northern Santa Barbara County (interior), and Santa Rosa (higher elevation, interior).

The error analysis results suggest that the clustering between vernal wetlands at Sedgwick and Del Sol and the remaining sites is robust up to a 50% error rate. Fig. 6 illustrates average Sorensen distance between Sedgwick and the other sites for 100 trials at the six different error levels. The plot

illustrates a prominent break between Sorensen distances of approximately 0.10 to 0.40 for Sedgwick and Del Sol and 0.55 to 0.85 for the remaining sites. The convergence of the lines toward the right indicate that the calculated distances remain largely the same regardless of error rates in the range evaluated. This occurs because these sites have few species in common, and even large percentages of

Distance (Objective Function)
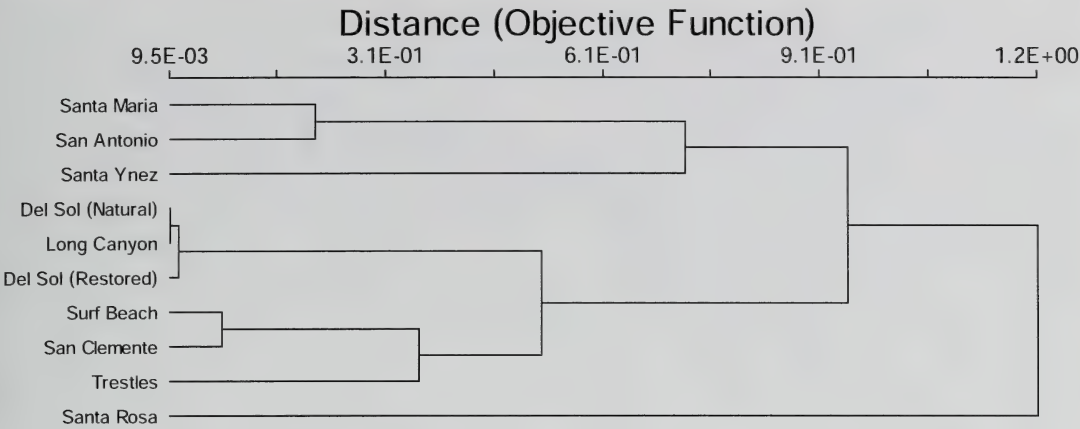
Fig. 4. Dendrogram for all 210 species across 12 sites created by agglomerative, polythetic clustering using the Sorensen distance measure and nearest neighbor linkage between groups. Distance function along the x-axis is a synthetic objective function based on the Sorensen distance measure.

additional species are unlikely to substantially increase their overall similarity. The greatest sensitivity was for the most similar sites, where additional species drove them substantially further apart (i.e., increased the number of unshared species between sites).

DISCUSSION

The Long Canyon vernal pond complex is a floristically rich habitat. Understanding this diversity in relationship to other vernal wetland habitats around the region is challenging. Initially, one might hypothesize that the wetlands would be most similar to the relatively nearby interior vernal pools and ponds of northern Santa Barbara County. This assessment is not supported by our observations or data provided by other studies. Based on the presence or absence of species, the Long Canyon ponds appear most similar to coastal vernal pools in the

Del Sol Preserve. Species composition next links the Long Canyon ponds to coastal vernal pools in southern California. Our analysis indicates that the Long Canyon ponds have low species-level similarity with other interior pools such as those nearby in northern Santa Barbara such as Santa Maria, San Antonio, and Santa Ynez or farther south on the Santa Rosa plateau. The small sample size available for this analysis limits our confidence in these conclusions, and it suggests that these findings can form a set of hypotheses for future work.

The species-level similarity of the Long Canyon and the Del Sol Preserve wetlands is somewhat surprising, as the wetlands vary in their geomorphology, landscape position, and surrounding habitat types. Both sites share a history of substantial human disturbance, including agriculture, grazing, and human trampling. Consequently, one hypothesis might hold that these disturbances can promote

Distance (Objective Function)
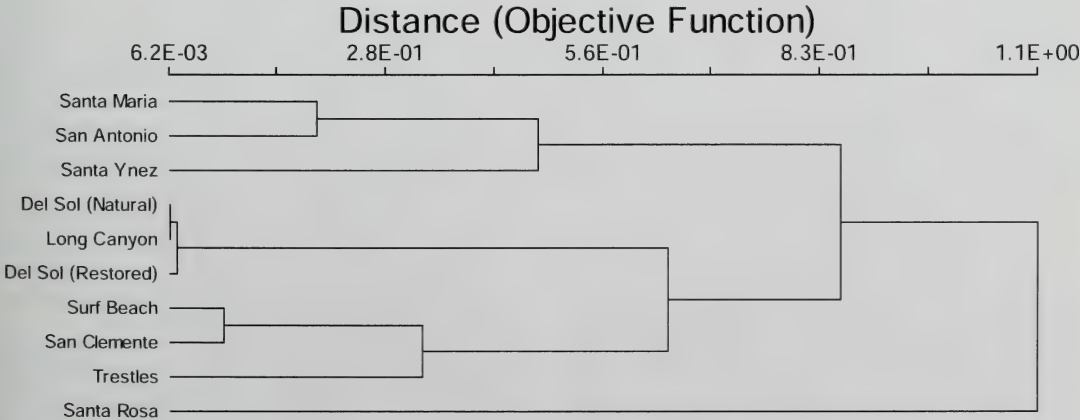
Fig. 5. Dendrogram for only the 133 wetland facultative or obligate species across 12 sites created by agglomerative, polythetic clustering using the Sorensen distance measure and nearest neighbor linkage between groups. Distance function along the x-axis is a synthetic objective function based on the Sorensen distance measure.
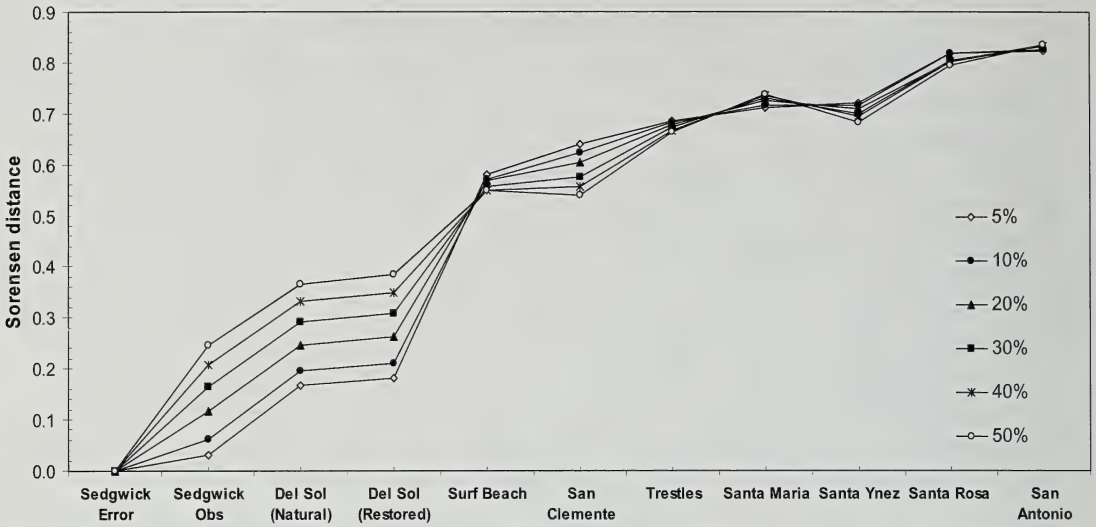
FIG. 6. Results from the simulated error and uncertainty analysis. Lines show the average Sorensen distance between each locality and the Sedgwick site arranged in rank order. Each line represents a different level of omission in our observations at Sedgwick ranging from 5% to 50% of the actual observed number of species. See "Error Analysis" section for details.

similar vegetation that is resistant to periodic mechanical stress and the introduction of potentially invasive species (Stone 1990). Alternatively, the floristic similarity between Long Canyon and Del Sol sites may result from similar hydrologic conditions resulting from very different climatic mechanisms. Cool, seasonally foggy coastal conditions produce relatively long-lasting and perennial wetlands along the coastal mesas of Santa Barbara (Ferren and Gevirtz 1990). The Long Canyon ponds experience higher temperatures but their water balance may be supplemented by seasonal groundwater contributions. The net result may be similar hydrologic conditions in very different climatic environments. Experimental evidence and field observations suggest that these hydrologic differences can structure vernal pool plant communities (Stone 1990; Bliss and Zedler 1998). Reconciling these competing hypotheses through future research will require greater access to vernal wetlands on private land for floristic surveys and experimental manipulations. This additional research will increase our ability to understand and predict vernal pool floristic composition and habitat value.

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APPENDIX 1. LIST OF SPECIES FOUND IN THE SEDGWICK RESERVE VERNAL POND COMPLEX AND OTHER LOCALITIES USED IN OUR FLORISTIC COMPARISONS. Species lists derived from Olson (1992) for the S.B. North County, Lanthrop and Throne (1976) for the Santa Rosa Plateau, Ferren and Pritchett (1988) for Del Sol, Rietner (1996) for San Onofre and San Clemente State Beaches, and this study for Sedgwick Reserve vernal ponds. Wetland status indicates association with wetland habitat: + for species listed by USFWS as wetland facultative or obligate and − for all others.

	Wetland status	Santa Barbara (Santa Maria)	Santa Barbara (San Antonio)	Santa Barbara (Santa Ynez)	Sedgwick vernal ponds	Del Sol natural pools	Del Sol restored pools	Santa Rosa Plateau	San Onofre (Surf Beach)	San Onofre (Trestles)	San Clemente State Beach
Agrostis viridis	−	0	0	0	0	0	0	0	0	0	1
Alopecurus howellii	−	1	1	0	0	0	0	0	0	0	0
Alopecurus saccatus	+	0	0	0	1	1	1	0	0	1	0
Alopecurus albus	+	0	0	0	0	0	0	0	0	1	1
Amaranthus blitoides	+	0	0	0	0	0	0	0	0	0	1
Amaranthus deflexus	−	0	0	0	0	0	0	0	1	0	1
Amblyopappus pusillus	+	0	0	0	1	1	1	0	0	0	1
Ambrosia psilostachya	+	0	0	0	1	1	1	0	1	1	1
Anagallis arvensis	+	0	0	0	0	0	0	0	0	0	1
Anagallis minima	−	0	1	0	1	1	1	0	1	0	0
Asclepias fascicularis	+	0	0	0	1	1	1	0	0	0	0
Atriplex lindleyi	−	0	0	0	0	0	0	0	1	0	1
Atriplex pacifica	+	0	0	0	0	0	0	0	0	0	1
Atriplex rosea	+	0	0	0	0	0	0	0	0	0	1
Atriplex semibaccata	+	0	0	1	1	1	0	0	1	0	1
Atriplex serenana	+	0	0	0	0	0	0	0	0	0	0
Atriplex triangularis	−	0	0	0	1	1	1	1	1	1	1
Avena barbata	−	0	0	0	1	1	1	0	1	1	1
Avena fatua	−	0	0	0	1	1	1	0	1	1	0
Baccharis glutinosa	−	0	0	1	0	0	1	0	1	0	0
Baccharis pilularis	−	1	0	1	1	0	1	1	1	1	1
Baccharis salicifolia	+	0	0	0	0	0	0	0	1	1	0
Blennosperma nanum	+	0	0	1	0	0	0	0	0	0	0
Bloomeria crocea	−	0	0	0	1	0	0	0	0	1	1
Boisduvalia densiflora	−	0	0	1	0	0	0	0	0	0	0
Brassica nigra	−	0	0	0	1	0	1	0	0	0	1
Briza minor	+	0	0	0	0	0	1	0	1	0	0
Brodiaea filifolia	+	0	0	0	0	0	0	1	0	0	0
Brodiacea jolonensis	−	0	0	0	0	0	0	0	0	1	1
Brodiaea orcuttii	+	0	0	0	0	1	0	1	0	0	1
Bromus diandrus	−	0	0	0	1	1	1	0	1	1	1
Bromus hordeaceus	+	0	0	0	1	1	1	0	1	1	1
Bromus madritensis subsp. rubens	−	0	0	1	0	0	0	0	1	1	1
Bromus mollis	−	0	0	0	0	0	0	0	0	0	0
Calandrinia ciliata	+	0	0	0	0	0	0	0	1	0	0

APPENDIX 1. CONTINUED.

	Wetland status	Santa Barbara (Santa Maria)	Santa Barbara (San Antonio)	Santa Barbara (Santa Ynez)	Sedgwick vernal ponds	Del Sol natural pools	Del Sol restored pools	Santa Rosa Plateau	San Onofre (Surf Beach)	San Onofre (Trestles)	San Clemente State Beach
Callitriche marginata	+	0	-	-	0	0	0	0	-	0	0
Calochortus splendens	-	0	-	-	0	0	0	0	-	0	-
Capsella bursa-pastoris	+	0	0	-	0	0	0	0	0	0	0
Cardamine californica var. *integrifolia*	-	0	0	0	0	0	0	0	0	0	-
Castilleja exserta	-	0	0	0	0	0	0	0	0	0	-
Centaurea melitensis	-	0	-	-	0	0	0	0	-	0	0
Centunculus minimus	+	0	0	0	-	0	0	0	0	-	-
Chamaesyce maculata	+	0	0	0	0	0	0	0	0	0	0
Chamomilla suaveolens	+	0	0	0	0	0	0	0	0	0	-
Chenopodium album	+	0	0	0	0	-	0	0	-	-	-
Chenopodium ambrosioides	+	0	0	0	0	0	0	0	0	0	0
Chlorogalum parviflorum	-	0	0	0	0	0	0	0	-	0	-
Chrysanthemum coronarium	-	0	0	0	0	0	0	0	0	0	0
Convolvulus arvensis	-	0	0	0	0	0	0	0	-	0	-
Conyza canadensis	+	0	-	-	0	0	0	0	0	0	0
Conyza coulteri	+	0	0	0	-	-	-	0	0	0	-
Cortaderia selloana	-	0	0	0	-	0	-	0	0	0	0
Cotula coronopifolia	+	-	-	0	-	0	-	0	-	0	0
Crassula aquatica	+	-	0	0	0	0	0	0	-	-	0
Crassula connata	+	0	0	0	0	0	0	0	-	0	0
Cressa truxillensis	+	0	0	0	0	0	0	0	-	0	-
Crypsis schoenoides	+	0	0	0	0	0	0	0	0	0	0
Cryptantha micromeres	-	0	0	0	-	0	0	0	0	0	0
Cynodon dactylon	+	0	0	-	-	0	-	0	-	0	-
Cyperus eragrostis	+	0	0	0	0	0	0	0	0	0	0
Cyperus esculentus	+	0	-	-	-	0	-	0	-	0	0
Deschampsia danthonioides	+	0	0	0	0	0	-	0	-	0	-
Dichelostemma capitatum	+	-	-	0	0	0	0	0	-	0	0
Distichlis spicata	+	0	0	-	0	-	-	-	-	-	-
Downingia bella	+	0	0	0	0	0	0	-	0	0	0
Downingia concolor var. *brevior*	+	0	0	0	0	0	0	0	0	0	-
Downingia cuspidata	+	0	0	0	0	0	0	0	0	0	0
Dudleya blochmaniae subsp. *blochmaniae*	-	0	0	0	0	0	0	0	0	0	0
Dudleya edulis	-	0	0	0	0	0	0	0	0	0	0
Dudleya lanceolata	-	-	0	-	0	0	0	0	0	0	0
Ehrharta erecta	-	-	-	-	0	-	-	-	-	-	-
Elatine brachysperma	+	-	-	0	0	-	-	0	-	0	0
Elatine californica	+	-	0	0	-	-	-	-	0	0	0
Eleocharis acicularis	+	-	0	0	-	-	-	-	0	0	0

APPENDIX 1. CONTINUED.

	Wetland status	Santa Barbara (Santa Maria)	Santa Barbara (San Antonio)	Santa Barbara (Santa Ynez)	Sedgwick vernal ponds	Del Sol natural pools	Del Sol restored pools	Santa Rosa Plateau	San Onofre (Surf Beach)	San Onofre (Trestles)	San Clemente State Beach
Eleocharis macrostachya	+	0	0	0	1	1	1	1	0	0	1
Eleocharis montevidensis	+	0	0	0	0	0	0	1	0	0	0
Eleocharis palustris	+	1	1	1	0	0	0	0	0	0	0
Eleocharis parishii	+	0	0	1	0	0	0	0	0	0	0
Elymus glaucus	–	0	0	0	1	1	0	0	0	0	0
Epilobium pygmaeum	+	0	0	0	1	0	0	0	1	0	0
Eremocarpus setigerus	–	0	0	1	0	1	1	0	1	0	1
Erodium botrys	+	0	0	0	0	1	0	0	1	0	1
Erodium cicutarium	–	0	0	0	0	0	1	0	1	1	1
Erodium moschatum	–	0	0	0	0	0	0	0	0	1	0
Eryngium armatum	+	0	0	1	0	0	0	0	1	0	0
Eryngium aristulatum subsp. parishii	+	0	0	0	1	1	0	1	0	0	0
Eryngium vaseyi	+	0	0	0	0	0	1	0	0	1	1
Euthamia occidentalis	–	0	0	0	0	0	0	0	0	1	0
Filago californica	–	0	0	0	0	0	0	0	0	0	0
Filago gallica	–	0	0	0	0	0	0	0	1	1	0
Foeniculum vulgare	–	0	0	0	0	0	0	0	1	0	1
Galium aparine	+	0	0	0	1	0	0	0	0	0	0
Gastridium ventricosum	+	0	0	0	0	1	0	0	1	1	1
Geranium dissectum	–	0	0	0	1	1	0	0	0	0	0
Glinus lotoides	+	0	0	0	0	0	1	0	0	0	0
Gnaphalium chilense	–	0	0	1	0	0	0	0	0	0	0
Gnaphalium luteo-album	+	0	0	0	0	0	0	0	1	1	1
Gnaphalium palustre	+	1	1	1	1	1	0	0	1	1	1
Grindelia camporum	+	0	0	0	0	0	1	0	0	0	1
Hainardia cylindrica	–	0	0	0	0	0	0	0	1	0	0
Harpagonella palmeri	–	0	0	0	0	0	0	0	0	0	1
Hedypnois cretica	–	0	0	0	0	0	0	0	0	0	1
Heleochloa schoenoides	+	0	0	1	1	0	0	0	0	0	0
Heliotropium curassavicum	–	0	0	1	1	0	0	0	1	0	0
Hemizonia fasciculata	+	0	0	0	0	1	0	0	0	0	1
Hemizonia paniculata	+	0	0	0	0	1	0	0	0	1	1
Hemizonia parryi subsp. australis	+	1	0	0	1	1	1	0	1	0	0
Hordeum brachyantherum subsp. brachyantherum	+	1	0	0	1	1	1	0	0	0	0
Hordeum brachyantherum subsp. californicum	+	0	0	0	1	1	1	0	1	0	0
Hordeum intercedens	+	0	0	0	0	0	0	0	0	0	1
Hordeum marinum subsp. gussoneanum	+	0	0	0	1	1	1	0	1	0	0
Hordeum murinum subsp. leporinum	–	0	0	0	0	0	0	0	1	1	1
Hypochaeris glabra	–	0	0	0	1	0	0	0	1	1	1

APPENDIX 1. CONTINUED.

	Wetland status	Santa Barbara (Santa Maria)	Santa Barbara (San Antonio)	Santa Barbara (Santa Ynez)	Sedgwick vernal ponds	Del Sol natural pools	Del Sol restored pools	Santa Rosa Plateau	San Onofre (Surf Beach)	San Onofre (Trestles)	San Clemente State Beach
Isocoma menziesii var. *menziesii*	+	0	0	0	0	1	0	0	1	0	1
Isocoma menziesii var. *vernonioides*	+	0	0	0	1	1	0	0	0	1	0
Isoetes howellii	+	0	0	0	0	0	0	1	0	0	0
Isoetes orcuttii	+	1	0	0	0	0	1	1	0	0	0
Juncus bufonis var. *bufonis*	+	0	0	1	1	1	1	1	1	1	1
Juncus mexicanus	+	0	0	0	0	0	1	0	0	0	0
Juncus occidentalis	+	1	0	0	0	0	1	0	0	0	0
Juncus phaeocephalus var. *phaeocephalus*	+	0	0	0	0	0	0	0	0	0	0
Juncus textilis	+	1	0	0	0	0	0	1	1	0	0
Lactuca serriola	+	0	0	0	0	0	0	0	0	0	1
Lamarckia aurea	+	0	0	0	0	0	0	0	0	0	0
Lasthenia californica	+	0	0	0	1	0	0	0	0	0	1
Layia platyglossa	–	0	0	0	0	0	0	0	0	0	0
Lepidium nitidum	+	0	0	0	0	0	0	0	0	0	1
Lilaea scilloides	+	1	1	0	0	0	0	1	0	0	0
Limnanthes gracilis subsp. *parishii*	+	0	0	0	0	0	0	1	0	0	0
Linanthus dianthiflorus	–	0	0	0	0	0	0	0	0	0	1
Linaria canadensis	–	0	0	0	0	0	0	0	0	0	0
Lippia nodiflora	+	0	0	0	0	0	0	0	1	0	1
Lolium multiflorum	+	0	0	1	0	0	0	0	0	0	0
Lolium perenne	+	1	0	0	0	0	0	0	1	0	1
Lupinus arboreus	–	0	0	0	0	0	0	0	0	0	0
Lythrum hyssopifolia	+	0	1	1	0	0	0	0	0	0	0
Malephora crocea	–	0	0	0	0	0	0	0	0	0	1
Malva parviflora	+	0	0	0	0	0	0	0	1	0	1
Malvella leprosa	+	0	0	0	0	0	0	0	0	0	0
Marrubium vulgare	+	0	0	0	0	0	0	1	0	0	0
Marsilea vestita	–	0	0	0	1	0	0	1	0	0	0
Medicago polymorpha	+	1	0	0	0	0	1	0	0	0	0
Mesembryanthemum nodiflorum	+	0	1	0	0	0	0	0	0	0	1
Micropus californicus	+	0	0	0	0	0	0	1	0	0	1
Microseris douglasii	–	0	0	0	0	0	0	0	0	0	0
Mimulus floribundus	+	1	0	0	0	0	0	0	0	0	0
Montia fontana	+	0	0	0	0	0	0	1	0	0	1
Muilla maritima	–	0	0	0	0	0	0	0	0	0	0
Myosurus minimus	+	0	0	0	0	0	1	1	0	0	1
Nassella lepida	–	0	0	0	0	0	0	0	0	0	0
Nassella pulchra	–	0	0	0	0	0	1	0	1	0	1
Navarretia atractyloides	–	0	0	1	0	0	0	0	0	0	0

APPENDIX 1. CONTINUED.

	Wetland status	Santa Barbara (Santa Maria)	Santa Barbara (San Antonio)	Santa Barbara (Santa Ynez)	Sedgwick vernal ponds	Del Sol natural pools	Del Sol restored pools	Santa Rosa Plateau	San Onofre (Surf Beach)	San Onofre (Trestles)	San Clemente State Beach
Navarretia prostrata	–	0	0	0	0	0	0	0	0	1	0
Navarretia hamata	–	0	0	0	0	0	0	1	0	0	0
Navarretia intertexta	+	0	0	0	0	0	0	1	0	0	0
Navarretia prostrata	+	0	0	0	0	0	0	1	0	0	0
Orcuttia californica	+	0	0	0	0	0	0	0	0	0	0
Orthocarpus densiflorus	–	1	0	0	0	0	0	0	1	0	1
Oxalis pescaprae	–	0	0	1	0	0	0	0	0	0	0
Petunia parviflora	+	0	0	0	1	0	0	0	0	0	0
Phalaris aquatica	+	0	0	0	0	1	1	0	0	0	0
Phalaris lemmonii	+	0	0	0	0	0	0	0	0	0	0
Phalaris minor	–	0	0	0	0	0	0	1	1	1	1
Phalaris paradoxa	+	0	0	1	0	0	0	1	0	0	1
Pilularia americana	+	1	0	0	0	0	0	0	0	0	1
Plagiobothrys acanthocarpus	+	0	0	0	0	0	0	0	1	1	0
Plagiobothrys collinus var. *fulvescens*	–	1	1	0	0	0	0	0	0	0	1
Plagiobothrys humistratus	+	1	0	0	0	0	0	1	0	0	0
Plagiobothrys leptocladus	+	0	0	0	0	0	0	0	0	0	0
Plagiobothrys nothofulvus	+	0	0	0	0	0	0	0	0	0	0
Plagiobothrys trachycarpa	+	1	1	1	0	1	1	0	0	0	0
Plagiobothrys undulatus	+	1	0	0	0	1	1	0	0	0	1
Plantago elongata	+	0	0	0	1	1	0	0	1	1	0
Plantago erecta	–	0	0	0	0	0	1	0	0	0	0
Plantago lanceolata	+	0	0	0	1	1	1	0	0	0	0
Plantago major	+	0	0	1	0	0	0	1	0	0	0
Plantago virginica	+	0	0	0	0	0	0	1	0	0	0
Pluchea odorata	–	0	0	0	0	0	0	0	0	0	0
Poa annua	+	0	0	0	1	1	0	0	1	1	1
Polygonum arenastrum	+	0	0	1	0	1	1	0	1	1	1
Polypogon monspeliensis	+	0	0	1	1	1	1	0	1	1	1
Psilocarpus brevissimus var. *brevissimus*	+	1	0	1	0	1	1	1	1	1	1
Psilocarpus tenellus var. *tenellus*	+	0	1	0	0	0	0	1	1	1	1
Ranunculus californicus	–	0	0	0	0	1	0	0	0	0	0
Raphanus sativus	–	0	0	0	0	0	1	0	0	0	1
Rhus integrifolia	–	0	0	1	1	0	0	0	1	1	0
Rorippa curvisiliqua	+	0	0	1	0	1	1	0	0	0	0
Rumex acetosella	+	0	0	1	0	1	1	1	0	0	0
Rumex crispus	+	0	1	0	0	1	1	1	1	1	1
Rumex angiocarpus	–	1	0	0	0	0	0	0	0	0	0
Salsola tragus	+	0	0	0	0	0	0	0	1	1	1

APPENDIX 1. CONTINUED.

	Wetland status	Santa Barbara (Santa Maria)	Santa Barbara (San Antonio)	Santa Barbara (Santa Ynez)	Sedgwick vernal ponds	Del Sol natural pools	Del Sol restored pools	Santa Rosa Plateau	San Onofre (Surf Beach)	San Onofre (Trestles)	San Clemente State Beach
Scirpus americanus	+	0	0	1	0	0	0	0	0	0	0
Scirpus cernuus	+	0	0	0	0	0	0	0	0	0	0
Senecio aphanactis	–	0	0	0	0	0	0	0	0	0	1
Senecio vulgaris	–	0	0	0	0	0	0	0	1	0	1
Sibara virginica	+	0	1	1	0	0	0	0	0	0	0
Sida leprosa	–	0	0	0	1	1	0	0	0	0	0
Silene gallica	–	0	0	0	0	0	0	0	0	0	1
Sisyrinchium bellum	+	0	0	0	1	0	0	0	1	0	1
Sonchus asper subsp. *asper*	+	0	0	0	0	0	0	0	0	0	1
Sonchus oleraceus	–	0	0	0	0	0	1	0	0	0	0
Spergularia arvensis	–	0	0	0	0	0	0	0	0	0	1
Spergularia bocconii	–	0	0	0	0	0	0	0	0	0	1
Spergularia macrotheca var. *macrotheca*	+	0	0	0	1	0	0	0	0	0	0
Spergularia ruba	+	1	0	0	0	0	0	0	0	0	1
Spergularia villosa	–	0	0	0	1	0	0	0	1	0	0
Stebbinsoseris heterocarpa	–	1	0	0	0	0	0	0	0	0	1
Tragopogon porrifolius	–	0	0	0	1	0	0	0	1	0	0
Trifolium depauperatum var. *amplectens*	+	0	0	0	0	0	0	0	0	0	1
Trifolium variegatum	+	0	0	0	0	0	0	0	0	0	0
Uropappus lindleyi	+	0	0	0	0	0	0	0	0	0	0
Verbena bracteata	+	1	1	1	0	1	0	0	1	0	1
Veronica peregrina subsp. *xalapensis*	–	1	0	0	1	1	1	0	0	0	1
Vicia benghalensis	+	0	0	0	0	1	0	0	0	0	0
Vicia sativa	+	0	0	0	0	0	0	0	0	0	0
Vulpia bromoides	+	0	0	0	0	0	0	0	0	0	0
Vulpia myuros var. *myuros*	+	0	0	0	0	0	0	0	1	1	1
Vulpia myuros var. *hirsuta*	+	0	0	0	0	0	0	0	1	1	1

USING MOLECULAR EVIDENCE TO ELUCIDATE RETICULATE EVOLUTION IN *OPUNTIA* (CACTACEAE)

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Abstract

The hypothesized natural interspecific hybrid origin of two cacti, *Opuntia* ×*rooneyi* and *O.* ×*spinosibacca*, has been investigated by a variety of non-molecular based techniques. Herein I explore DNA sequence and random amplified polymorphic DNA (RAPD) banding pattern data as it relates to these two cases of putative hybridization. Traditional parsimony-based analyses of nuclear ribosomal and chloroplast DNA sequences do not resolve the phylogenetic position of these two species among closely-related taxa, but a median network analysis is presented that yields an approach to interpreting these relationships. Finally, an analysis of RAPD banding pattern data provides evidence of the additive genetic pattern expected for these two interspecific hybrids. These results support the inferences of non-molecular based studies.

Key Words: Hybridization, parsimony analysis, median network, *Opuntia*, RAPDs.

Hybridization has long been thought to contribute to biodiversity, often leading to the formation of new taxa (Keck 1937; Grant 1954; Lewis and Lewis 1955; Stebbins 1957, among many others). Many types of data have been used to infer hybrid origin of taxa. Morphological data far surpass any other data type in giving researchers inference into hybrid origin, but geographical, ecological, biosystematic, and cytological data have also given insight into reticulate speciation. More recent work downplays the importance of these data types, instead stressing that (macromolecular) genetic evidence confers a greater (and independent) power of inference (Gallez and Gottlieb 1982; Barker et al. 1996; Allan et al. 1997). Putative hybrid taxa have been examined with a variety of genetic techniques, including enzymatic methods (Gallez and Gottlieb 1982; Barrington 1990; Krutovskii and Bergmann 1995), restriction fragment length polymorphisms (Kron et al. 1993; Milne et al. 1999), random amplified polymorphic DNA (RAPD) data (Barker et al. 1996; Díaz Lifante and Aguinagalde 1996; Padgett et al. 1998), and DNA sequence data (Alice et al. 2001).

Cacti illustrate this progression of methodologies particularly well. Hybridization is a well-established means of establishing novel taxa of Cactaceae (Moran 1962; Rowley 1982, 1994; Powell et al. 1991; Powell 1995, 1999). Hybridization as a means of speciation is especially common within the subfamily Opuntioideae (Benson and Walkington 1965; Grant and Grant 1971, 1979; Baker and Pinkava 1987, 1999; Griffith 2001a, b; Pinkava 2002; Hernandez et al. in press). Many of the above types of evidence have previously been used to investigate the hybrid origins of opuntioid taxa, including morphological (Walkington 1966; Grant and Grant 1979; Baker and Pinkava 1987; Hernandez et al. in press), phytochemical (Walkington 1966), geographical (Hernandez et al. in press), artificial hybridization (Griffith 2001b), cytological evidence (Baker and Pinkava 1987; Pinkava and Parfitt 1988), and more recently, molecular evidence in the form of RAPD banding pattern data (Mayer et al. 2000).

At least two Northern Chihuahuan Desert taxa of *Opuntia* sensu stricto are believed to be of hybrid origin. *Opuntia* ×*spinosibacca* is believed to be the result of hybridization between *O. camanchica* and *O. aureispina* (Pinkava and Parfitt 1988; Powell 1998; Powell and Weedin 2001), and *O.* ×*rooneyi* is thought to be the result of hybridization between *O. aureispina* and *O. macrocentra* (Griffith 2001a). The ranges of these putative hybrid taxa intersect with those of the putative parental taxa (Fig. 1). In addition, the hybrid taxa exhibit intermediate morphology between their putative parents (Table 1), and in the case of *O.* ×*spinosibacca,* intermediate karyotype; *O. camanchica* is hexaploid ($2n = 66$), *O. aureispina* is diploid ($2n = 22$), and *O.* ×*spinosibacca* is tetraploid ($2n = 44$) (Pinkava and Parfitt 1988; Powell and Weedin 2001). For the current study, I explored the putative hybrid origin of *O.* ×*spinosibacca* and *O.* ×*rooneyi* through the analysis of DNA sequence data and RAPD banding pattern data.

Materials and Methods

I extracted total genomic DNA from specimens of *Opuntia* representing the hybrid taxa *O.* ×*spinosibacca* and *O.* ×*rooneyi,* and putative parental

TABLE 1. MORPHOLOGICAL CHARACTERS OF *OPUNTIA* SPECIES INCLUDED IN THIS STUDY. Data adapted from Powell (1998) and Griffith (2001a).

	Central spines per areole, length	Radial spines per areole, length	Spination	Spine color	Pad color
O. macrocentra	1–2, 7–12 cm	0	most distal areoles	black, white tips	purple
O. ×*rooneyi*	2–3, 4–5 cm	1–4, to 2 cm	upper two thirds of areoles	brown to red, yellow tips	green-purple
O. aureispina	3–6, 2–6 cm	2–7, to 3 cm	over entire cladode	uniformly yellow	yellow-green
O. ×*spinosibacca*	2–5, to 7 cm	0	most of cladode	red to brown	yellow-green
O. camanchica	1–3, 3–7 cm	0	upper half of cladode	dark brown	bluish-green

taxa. Additional DNA extractions were performed, for a total of 29 specimens of opuntioid taxa for use in phylogenetic comparisons (Table 2). I employed a protocol (Griffith and Porter 2003) for nucleic acid extraction from mucilaginous tissues, modified from Doyle and Doyle (1987). Amplification of templates for sequencing was performed with the primers *trnE, trnF* (Taberlet et al. 1991), ITS5, and ITS4 (White et al. 1990). Thermal cycling parameters for the nrITS and *trnL-F* regions follow Columbus et al. (1998) and Porter et al. (2000), respectively. Templates were purified by precipitation in PEG (Morgan and Soltis 1993), and washing once in 100 µl 80% ethanol. Purified templates were then sequenced directly with 6 primers: ITS5, ITS4, ITS3, and ITS2 (White et al. 1990), *trnE* and *trnF* (Taberlet et al. 1991). For cycle sequencing, I used "Big Dye" chemistry (Applied Biosystems), according to the manufacturer's specifications. An Applied Biosystems 3100 Genetic Analyzer gathered all DNA sequence data. Raw sequences were assembled into contigs and edited using Sequencer v4.1 (Gene Codes Corporation). The program Se-Al (Rambaut 1996) assisted with man-

1. O. **x**rooneyi
2. O. aureispina
3. O. **x**spinosibacca
4. O. camanchica
5. O. macrocentra
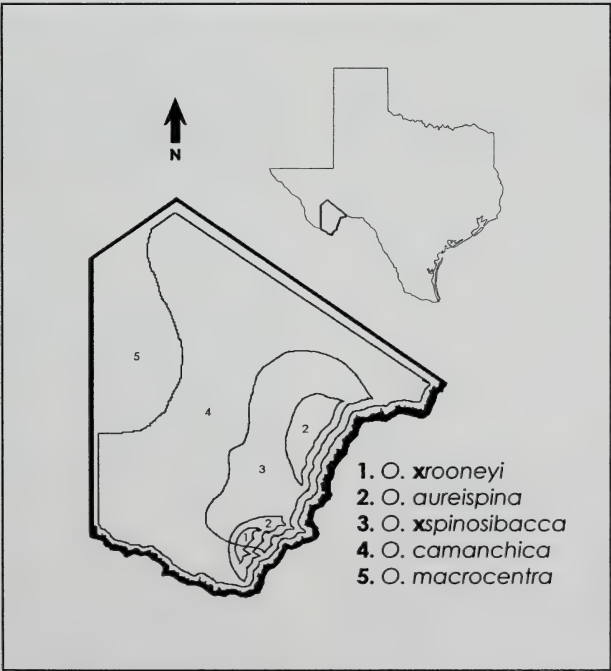
FIG. 1. Ranges of two putative hybrid *Opuntia, O.* ×*rooneyi* and *O.* ×*spinosibacca,* and putative parental taxa *O. aureispina, O. camanchica,* and *O. macrocentra* in Brewster County, Texas, USA. *Opuntia macrocentra* is distributed throughout the county, and *O. camanchica* is found throughout, except the northwestern portion; the other taxa are more restricted in range. Adapted from Griffith (2000).

TABLE 2. SPECIMENS USED FOR MOLECULAR ANALYSES. DBG = Desert Botanical Garden, Phoenix, Arizona; HBG = Huntington Botanical Gardens, San Marino, California; MG = Mesa Garden, Belen, New Mexico.

Taxon	Specimen	Voucher
Brasiliopuntia brasiliensis (Wildenow) Berger	DBG 1990-0559	
Consolea spinosississima (Miller) Lemaire	DBG 1995-0389	
Nopalea cochenillifera (L.) Salm-Dyck	DBG 1997-0395	
Miqueliopuntia miquelii (Monville) Ritter	DBG 1997-0129	
Opuntia aureispina (Heil & Brack) Pinkava & Parfitt	*Griffith 73*	SRSC
Opuntia boldinghii Britton & Rose	DBG 1977-0391	
Opuntia bravoana Baxter	HBG 47063	
Opuntia camanchica Engelmann & Bigelow	*Weedin 374*	SRSC
Opuntia chisosensis (Anthony) D. J. Ferguson	*Powell 5771*	SRSC
Opuntia durangensis Britton & Rose	*Griffith 156*	RSA
Opuntia engelmannii Salm-Dyck ex Engelmann	*Powell 6009*	SRSC
Opuntia erinacea Engelmann & Bigelow	*Honer 658*	RSA
Opuntia ficus-indica (L.) Miller	*Griffith 326*	RSA
Opuntia lindheimeri Engelmann	*Weedin 1670*	SRSC
Opuntia macrocentra Engelmann	*Raun 94-01*	SRSC
Opuntia megasperma Howell	DBG 1994-0075	
Opuntia phaeacantha Engelmann	*Griffith 214*	RSA
Opuntia pubescens Wendland ex Pfeiffer	*Griffith 308*	RSA
Opuntia pumila Rose	DBG 1999-0035	
Opuntia ×rooneyi M. P. Griffith	*Griffith 71*	SRSC
Opuntia santa-rita (Griffiths & Hare) Rose	*Griffith 227*	RSA
Opuntia setispina Engelmann ex Salm-Dyck	*Griffith 145*	RSA
Opuntia ×spinosibacca Anthony	*Hughes 801*	SRSC
Opuntia strigil Engelmann	*Powell 6008*	SRSC
Opuntia sulfurea G. Don	DBG 1995-0372	
Opuntia stricta (Haworth) Haworth	HBG 71091-1	
Pterocactus decipiens Gürke	MG 1179.2	
Pterocactus valentinii Spegazzini	MG 1179.68	
Tunilla corrugata (Salm-Dyck) Hunt & Iliff	*Hunt 66371*	DES

ual alignment of consensus sequences. Phylogenetic relationships among sequences were determined by a heuristic search of the sequence data using Fitch parsimony, as implemented by PAUP 4.10b (Swofford 1998). Estimations of confidence in the recovered clades were obtained by bootstrapping (Felsenstein 1985) with 1,000 pseudoreplicates, as implemented in PAUP. In addition, the median network (Bandelt et al. 1995) of all possible pathways among these sequences was constructed using Spectronet v1.2 (Langton 2001), pruned to k=3 (Bandelt et al. 1995) to enable interpretation.

The RAPD method (Williams et al. 1990) was also used to scan for genetic additivity. Stringent amplification, visualization, and scoring conditions were maintained to ensure repeatability (Hadrys et al. 1992). Each 25 μl reaction contained PCR buffer at 1.5 mM MgCl, 2.5 mM of each dNTP, 20 mM of a specific primer, 1 unit of *Taq* polymerase, and 10 ng of template DNA. A 96-well Robocycler (Strategene, Inc.) provided thermal cycling: 94°C for two minutes, followed by 44 cycles at 94°C for 1 min, 40°C for 1 min, and 72°C for 2 min, and a final extension of 7 min at 72°C. Fifteen 10 mer primers were used for RAPD amplifications: Op-B-18, Op-D-2, Op-D-5, UBC-101, UBC-103, UBC-108, UBC-111, UBC-149, UBC-165, UBC-188, UBC-190, UBC-417, UBC-446, and UBC-489 (Fritsch et al. 1993). Entire 25 μl reactions were loaded onto 2.0% agarose gels, immersed in 1× TBE, and electrophorectically separated with 30 mV for 12 h. Gels were stained with ethidium bromide for 15 min, destained in water for 30 min, visualized under UV light, and photographed. Rf values of observed bands were compared with Rf values of known molecular weight markers to estimate weight of observed amplicons. For each primer, each band was scored as either present or absent for each molecular weight. Only markers which could be scored unambiguously for presence or absence were used to estimate additivity (Friar et al. 1996; Robichaux et al. 1997). Banding patterns were interpreted manually, and statistically analyzed for correlation and factor analysis using Statview 5.0.1 for Windows (SAS corporation, Chicago, IL).

RESULTS AND DISCUSSION

Phylogenetic analysis of the aligned DNA data matrix yielded a well supported (94% bootstrap) clade of *Opuntia* native to the Chihuahuan and Sonoran Desert regions of North America (with the notable exception of *O. boldinghii,* a native of the Caribbean), which includes both putative hybrid taxa, as well as all three putative parental taxa (Fig. 2). The combined ITS and *trnL-F* data do not resolve the relationships among this monophyletic
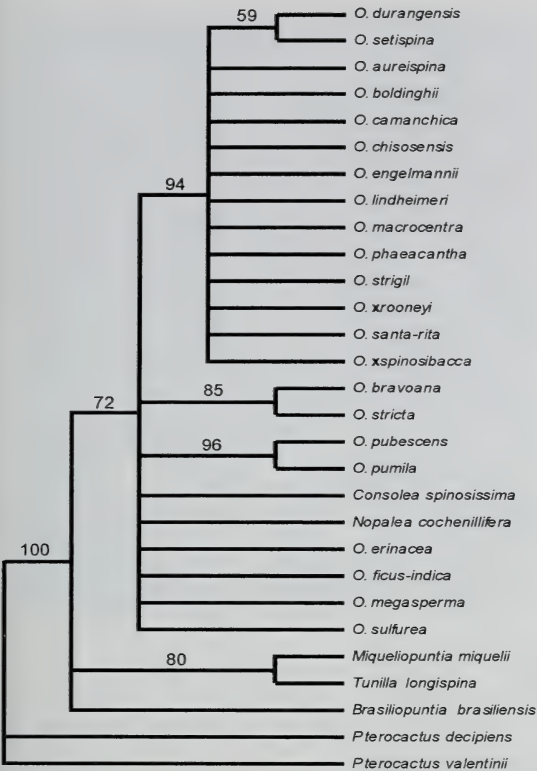
FIG. 2.   Phylogenetic analysis of *Opuntia* ×*rooneyi*, *O.* ×*spinosibacca*, putative parental taxa, and related taxa. A strict consensus of 931,500 most parsimonious trees produced by the heuristic search of the combined ITS and *trnL-F* sequence data. Figures above branches represent bootstrap percentages above 50. With uninformative characters excluded, length = 51; CI = 0.8763; RI = 0.9048.

group. Median network analysis is useful for resolving relationships between closely related individuals, however (Bandelt et al. 1999); this analysis of the same data produced an unrooted network showing all most parsimonious pathways between the ITS and *trnL-F* sequences for these taxa (Fig. 3). Note that sequences obtained from the putative hybrid taxa *O.* ×*rooneyi* and *O.* ×*spinosibacca* are very proximal to those obtained from putative parental taxa. *Opuntia* ×*rooneyi* is merely one step removed from both putative parental taxa *O. aureispina* and *O. macrocentra*. *Opuntia* ×*spinosibacca* is one step removed from one putative hexaploid parent, *O. camanchica*, and two steps removed (via one of two shortest pathways) from another putative hexaploid parent, *O. phaeacantha* var. *major,* and the putative diploid parent, *O. aureispina*. Although this analysis cannot resolve reticulate evolution (via genetic additivity, *sensu* Gallez and Gottlieb 1982), the short pathways between the putative parental and hybrid taxa suggest a close relationship among these entities, consistent

TABLE 3.   SUMMARY OF OBSERVED RAPD BANDING FOR *O.* ×*ROONEYI* AND PUTATIVE PARENTAL TAXA.

	O. ×*rooneyi*	*O. aurei-spina*	*O. macro-centra*
Total bands:	53	26	44
Unique bands:	9	0	13
Shared bands with *O.* ×*rooneyi*	—	21	31
Private bands with *O.* ×*rooneyi*	—	10	19
Private bands between *O. aureispina* and *O. macrocentra*		1	

with the morphological, geographical, and (in the case of *O.* ×*spinosibacca*) cytological evidence of hybridization.

Banding patterns obtained by RAPD analysis can be used to screen for genetic additivity (Mayer et al. 2000). Of the fifteen primers used for the RAPD analysis, a total of 53 bands were scored for *O.* ×*rooneyi* (Table 3), and 51 were scored for *O.* ×*spinosibacca* (Table 4). An example of the banding pattern observed by amplification with a specific primer is presented in Fig. 4. A correlation matrix of the banding pattern data is presented in Table 5, and a factor plot of these data is presented in Fig. 5. The two putative parents of *O.* ×*rooneyi* (*O. aureispina* and *O. macrocentra*) had a total of 26 and 44 bands present, respectively. Few unique bands (17% of the total) were observed for this complex, and a high proportion (73%) of the bands present in the parental taxa was also observed in *O.* ×*rooneyi*. More relevantly, 41% of the bands observed in the parental taxa are privately shared with the putative hybrid *O.* ×*rooneyi,* while only 1 parental band (1.4%) is privately shared between the parental taxa (Table 3). Thus, while a sizable portion of bands observed in the putative hybrid has identity with the putative parents, the parents have little identity with each other. Additionally, high correlation with *O. aureispina* and *O. macrocentra* was found for *O.* ×*rooneyi* when analyzed

TABLE 4.   SUMMARY OF OBSERVED RAPD BANDING FOR *O.* ×*SPINOSIBACCA* AND PUTATIVE PARENTAL TAXA.

	O. × *spino-sibacca*	*O. aurei-spina*	*O. caman-chica*
Total bands:	51	26	46
Unique bands:	12	7	9
Shared bands with *O.* ×*spinosibacca*	—	16	33
Private bands with *O.* ×*spinosibacca*	—	6	23
Private bands between *O. aureispina* and *O. camanchica*		3	
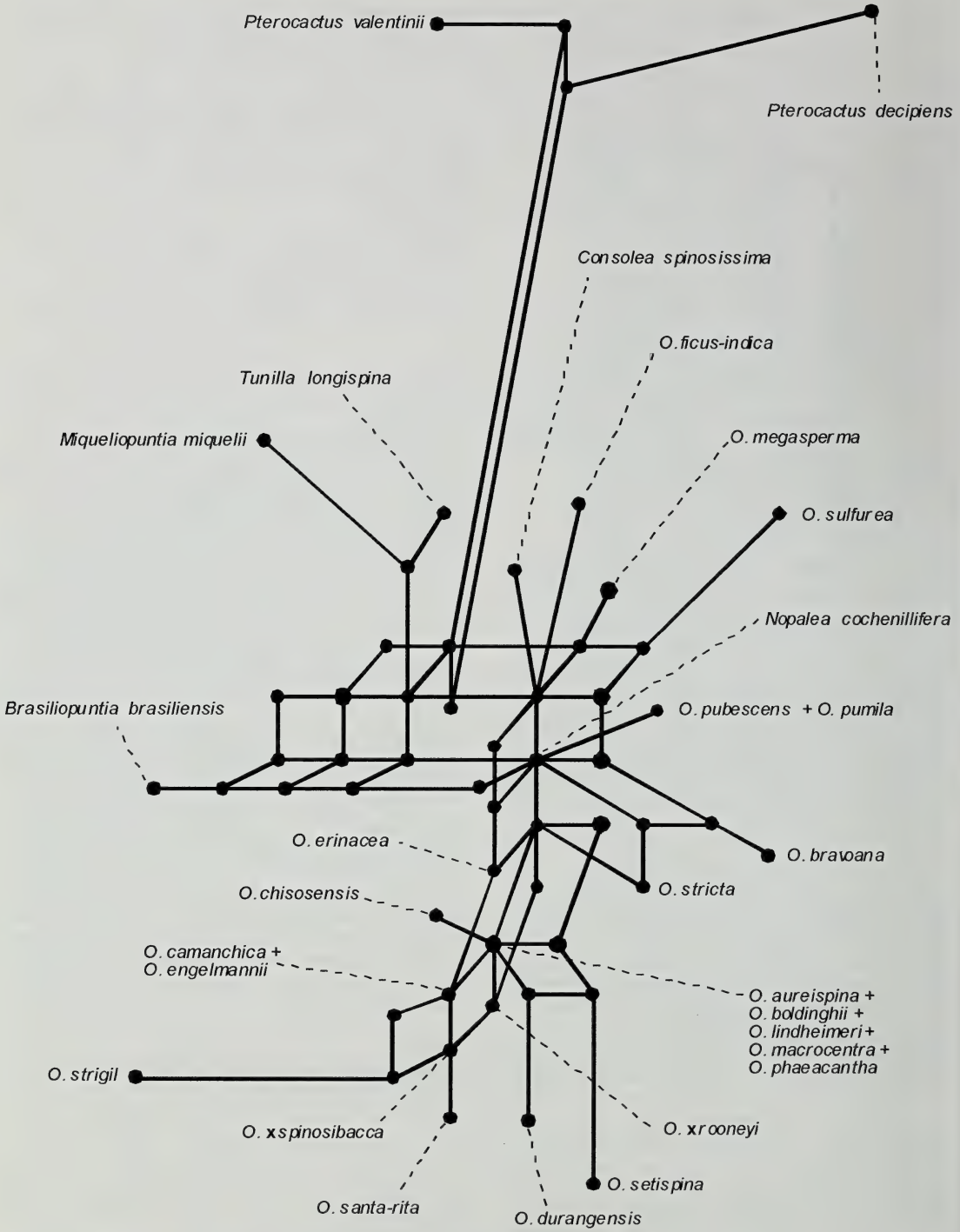
FIG. 3. Median network showing all most-parsimonious pathways between the combined ITS and *trnL-F* sequences for the sampled *Opuntia* taxa (Table 2). Points that correspond to observed sequences are labeled with those taxa; unlabeled points represent hypothetical sequences that must be "passed through" in order to reach other observed sequences.

FIG. 4. Example RAPD amplification: six specimens of *Opuntia* amplified with primer Op-B-18. Lanes are as follows: 1) molecular weight markers; 2) *O. aureispina*; 3) *O. macrocentra*; 4) *O. ×rooneyi*; 5) *O. macrocentra*; 6) *O. camanchica*; 7) *O. ×spinosibacca*.

hybrid origin of that taxon. For this hybrid complex, a total of 28 unique bands were observed overall (22% of the total). The putative parents *O. camanchica* and *O. aureispina* shared a total of 33 (71%) and 16 (62%) bands respectively with the putative hybrid, and 23 (50%) and 6 (23%) of those bands (respectively) were privately shared. Only 3 (4%) of the parental bands are privately shared between the parental taxa. It is interesting to note that a much greater number of bands present in *O. ×spinosibacca* have identity with one parent, *O. camanchica*. This strong identity is also apparent in the factor plot (Fig. 5) and correlation matrix (Table 5). The RAPD banding pattern of *O. ×spinosibacca* correlates positively with both putative parents, and correlates negatively with the other two taxa (Table 5). As in the example above, these data are not conclusive proof of hybrid origin on their own, but in context with the morphological intermediacy (Powell 1998), cytogenetic intermediacy (Pinkava and Parfitt 1988; Powell and Weedin 2001), and the phylogenetic and network relationships presented above, *O. ×spinosibacca* certainly seems to represent a product of reticulate evolution.

Further investigations, involving increased sample sizes, increased sampling of genes, and perhaps other genetic techniques may give increased insight into the exact nature of the hybridization events investigated here; and perhaps growing artificial F1 hybrids to maturity (as in Powell et al. 1991) would also yield valuable information. A broad study using all of the above techniques with very inclusive sampling would be a desirable project that could greatly expand our understanding of how reticulate evolution occurs in cacti. While molecular data is often useful for evaluating hybrid origins of taxa, such investigations may greatly benefit from the integration of as many additional data types as possible (see also Pinkava 2002).

statistically (Table 5), while negative correlation was observed with *O. camanchica* and *O. ×spinosibacca*. A factor plot of these data (Fig. 5) shows a proximal and somewhat intermediate position for *O. ×rooneyi* between its putative parents. Although these data are consistent with the additive genetic pattern expected for hybrid speciation, the restricted sample warrants caution against interpreting these results alone as conclusive evidence of the hybrid origin of *O. ×rooneyi*. However, when these data are viewed in context with the morphological intermediacy (Griffith 2001a), observed interfertility of the parental taxa (Griffith 2001b), and the phylogenetic and network analyses presented above, the hypothesis of hybrid origin for *O. ×rooneyi* is difficult to reject.

Similarly, RAPD banding patterns observed for *O. ×spinosibacca* (Table 4) are consistent with the

TABLE 5. CORRELATION MATRIX OF RAPD BANDING PATTERN DATA. [1] *macro.* = *O. macrocentra*; *roon.* = *O. ×rooneyi*; *aurei.* = *O. aureispina*; *spino.* = *O. ×spinosibacca*; *caman.* = *O. camanchica*.

	macro.[1]	*roon.*	*aurei.*	*spino.*	*caman.*
O. camanchica	−.131	−.040	−.070	.338	1.000
O. ×spinosibacca	−.154	−.045	.014	1.000	
O. aureispina	−.046	.317	1.000		
O. ×rooneyi	.277	1.000			
O. macrocentra	1.000				
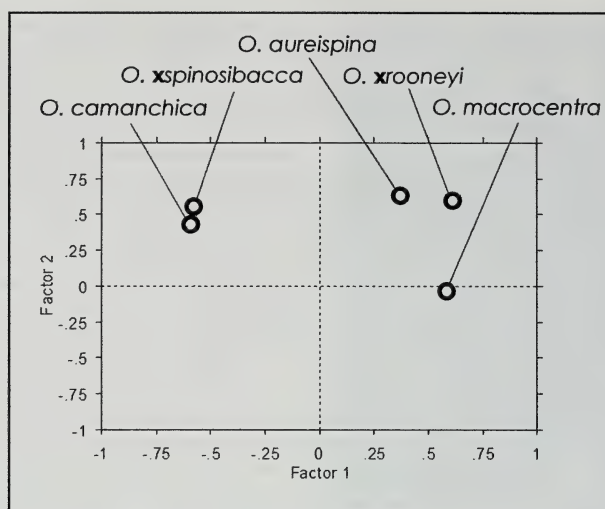
Fig. 5.   Unrotated factor plot of RAPD banding pattern data observed for the five taxa studied. *Opuntia* ×*spinosibacca* groups closely with *O. camanchica,* a putative parent. The next most proximal taxon is *O. aureispina,* the other putative parent. *Opuntia* ×*rooneyi* is proximal to and intermediate between the putative parental taxa *O. aureispina* and *O. macrocentra.*

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REPRODUCTIVE ISOLATION AND HYBRIDIZATION BETWEEN TWO MILKWEEDS (*ASCLEPIAS FASCICULARIS* AND *A. SPECIOSA,* ASCLEPIADACEAE)

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ABSTRACT

This study examines reproductive isolation and the potential for hybridization between *Asclepias speciosa* Torr. and *Asclepias fascicularis* Dcne., two species of milkweed that co-occur in the Willamette Valley and in the Columbia River Gorge in Oregon. Since these species are ecologically and geographically sympatric, we investigated whether extrinsic differences in flowering time, insect visitors, and the sizes of floral structures might serve as pre-mating barriers to hybridization. Floral and vegetative characters were measured to confirm species distinctions and to test for possible character displacement in sympatric versus isolated populations of both species. The sizes of pollinia and stigmatic chambers differed significantly between species suggesting strong mechanical isolation in combinations with large-flowered *A. speciosa* as the pollen donor. Additional post-mating barriers also exist since experimental crosses between *A. speciosa* and *A. fascicularis* yielded seed only with *A. fascicularis* as the maternal parent. Interspecific pollinations yielded higher fruit-set (35%) than conspecific pollinations (13%) of *A. fascicularis,* suggesting that pollen tubes of larger-flowered *A. speciosa* may be more effective in traversing the style, or that insufficient compatible genotypes exist within small, fragmented populations of these species. Seeds from the successful hybrid crosses were comparable to *A. speciosa* in germination and produced viable hybrid offspring.

Key Words: *Asclepias,* hybrid, milkweed, reproductive isolation, character displacement.

Interspecific hybridization is not only prevalent in plants, but it has contributed significantly to their evolution, with a diversity of outcomes in natural populations (Anderson 1948; Heiser 1973; Arnold 1992, 1997; Rieseberg 1997). Rare species may risk either genetic swamping or genic infiltration after hybridization with widespread native or introduced congeners (Abbott 1992; Ellstrand and Elam 1993; Runyeon-Lager and Prentice 2000). However, new hybrid species have also arisen and become stabilized through novel chromosomal combinations and habitat divergence (Arnold 1994; Rieseberg et al. 1995; Wolfe et al. 1998; Freeman and Herron 2001; Welch and Rieseberg 2002). In *Helianthus,* at least three western sunflowers (*H. anomalous, H. deserticola,* and *H. paradoxus*) are the products of independent, diploid hybrid speciation events between the same two species, *H. annuus* and *H. petiolaris* (Schwarzbach and Rieseberg 2002). The extent to which hybrids form also influences whether closely related taxa continue to diverge, reinforcing and finalizing speciation (Levin 1978; Wolf et al. 2001).

Successful hybridization requires that all stages of the reproductive process occur, including interspecific pollination and post-zygotic events. Presently the role of reproductive isolating barriers (RIBs) in speciation is being widely debated as a gene specific or genome wide phenomenon, as a

by-product of divergence or causative factor in species formation, and in terms of the relative roles and origin of pre-mating versus post-mating isolation (Orr 2001; Mayr 2001; Van Alphen and Seehausen 2001; Wu 2001a, 2001b). In any case, natural selection appears to have had a pervasive role in the evolution of reproductive isolation, whose extent is often correlated with levels of genetic divergence (Hodges and Arnold 1994; Fitzpatrick 2002). RIBs may arise as a byproduct of divergent selection or genetic drift, or in the case of pre-mating barriers, as a result of selection against hybridization or to reduce interspecific competition for pollinators (Endler 1989; Judd et al. 1999). These processes can also lead to character displacement, whereby individuals in sympatric populations show greater divergence than in allopatric populations where plants are not directly competing for resources, or are less affected by any reductions in fitness resulting from hybridization (Levin 1985).

The prevalence of spontaneous hybridization varies greatly among plant families (Ellstrand et al. 1996). Milkweeds (*Asclepias*) offer an ideal study system to examine diverse forms of reproductive isolation due to the rarity of hybridization among species in this genus. Of approximately 120 species of *Asclepias* known in North America, only 12 cases of interspecific hybridization are known (Wyatt and Broyles 1994). Just two instances of natural hybridization are widely known: 1) hybrid zones between the largely allopatric common milkweed, *A. syriaca,* prevalent in eastern North America, and *A. speciosa,* which occurs west of the Mississippi

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River (Thomson and Wagner 1978); 2) hybrid swarms occurring in ecotones between the field and woodland habitats of *A. syriaca* and its geographically sympatric congener, *A. exaltata*. In this case, extensive morphological study, crossing experiments, flavonoid chemistry, isozyme and DNA analyses have provided strong evidence of hybridization and introgression (Kephart et al. 1988; Wyatt and Hunt 1991; Wyatt and Broyles 1992). However, sympatric asclepiads rarely hybridize, and are often isolated by both pre-mating and post-mating barriers (Kephart 1981, 1983; Wyatt and Broyles 1994; Broyles et al. 1996).

Milkweeds are fairly common in North America, but co-occurring western species have been little studied despite the possibility of hybrids. Thus, this study examines the likelihood of hybridization between two relatively widespread western species, *A. fascicularis* (narrow-leaved milkweed) and *A. speciosa* (showy milkweed). We know of no comparative studies of these species although they grow in similar habitats and occur sympatrically in the Pacific Northwest. Our study sites in Oregon incorporate unispecific and mixed populations of both milkweeds in two different geographic provinces, the western Willamette Valley and eastern Columbia River Basin.

The observations and experimental manipulations in this paper address the potential for pre-mating and post-mating reproductive barriers to hybridization. Two focal questions guided the study: 1) Do intrinsic and extrinsic barriers to hybridization operate in natural populations of *A. fascicularis* and *A. speciosa*? 2) Is character displacement evident in co-occurring populations of these species? We explored factors considered most likely to serve as RIBs based on previous field observations including: differences in flowering phenology, size differences in reproductive structures that might lead to mechanical or floral isolation, and the possibility of post-zygotic failure. Prior to this study, no putative hybrids were known for northwestern milkweeds. This investigation also differs from most studies of hybridization in *Asclepias* in that these particular species are both ecologically *and* geographically sympatric. Because of the strong sympatry and apparent absence of hybrids, we hypothesized that intrinsic, post-mating barriers to hybridization are present, and that character displacement was unlikely unless considerable overlap in flowering time or pollinators occurred.

Study system. The complex floral structure and pollinating apparatus are assumed to play a major role in preventing hybridization and maintaining species barriers among milkweeds (Woodson 1954; Kephart and Heiser 1980; Wyatt and Broyles 1994). The morphology of asclepiad flowers is unique as a result of the positions of stigmas and anthers, as well as the means of pollen dispersal (Kunze 1990; Fishbein 2001). Nectar accumulates in five open hoods that alternate with five stigmatic chambers that are formed by the wing-like elaborations of adjacent anthers. Each pair of adjoining anther wings creates a slit that receives an incoming pollinium, which is transported by insects and contains the pollen (Morse 1985). The pollinia are produced within the anthers in pairs that are connected by translator arms to a grooved corpusculum. Together the two pollinia, translator arms, and corpusculum are called a pollinarium (Bookman 1981).

Pollination in *Asclepias* is accomplished by diverse hymenopterans and lepidopterans whose actions involve two important steps: pollinarium removal and pollinium insertion (Robertson 1928; Kephart 1983). Removal occurs when a groove in the corpusculum entraps the hairs or appendages of a nectar-probing insect. Thereafter, the translator arms of the pollinarium twist, rotating the attached pollinia 90°, and facilitating insertion into the stigmatic chamber of another flower. Once a pollinium is inserted, its pollen tubes emerge, traverse the stylar canal to the ovary, and initiate seed maturation and the formation of a follicle, or fruit (Wyatt and Broyles 1994).

METHODS

Study sites. Potential study populations of the two milkweed species were initially located using herbarium records, referrals from scientists and landowners, and exploration. Those chosen for field study occurred in the Willamette Valley of western Oregon, and near The Dalles in the eastern section of the Columbia River Gorge (Table 1). We sampled two geographically diverse areas so as to evaluate hybridization in varied ecological zones. The eastern Oregon sites fall within the Columbia Basin Physiographic Province, where xerophytic climatic conditions prevail relative to the Willamette Valley; the west-east transition is accompanied by a shift in the dominant trees from mixed *Pseudotsuga menziesii-Abies grandis* associations to those of *Pinus ponderosa-Pseudotsuga menziesii* (Franklin and Dryness 1988). Both *A. speciosa* and *A. fascicularis* grow primarily in open grassland, though plants sometimes occur in partial shade within riparian zones (e.g., at Fulton Farm) or in open savannas where trees are small (e.g., Wilson site). We selected study sites to include co-occurring (mixed) as well as unispecific populations of *A. speciosa* and *A. fascicularis* (Table 1). Hybrids were not evident in any populations based on obvious morphological differences: showy milkweed (*A. speciosa*) bears pendent, large flowered umbels on unbranched stems with opposite, broadly ovate leaves. In contrast, *A. fascicularis* has narrow, lanceolate leaves and microphyllous branches; its smaller flowers occur in erect umbels on branched stems (Woodson 1954). Voucher specimens representing both species are deposited in the herbaria of Willamette University (WILLU) and Oregon State University (OSC).

TABLE 1. LOCATION OF UNISPECIFIC AND MIXED POPULATIONS OF *A. FASCICULARIS* AND *A. SPECIOSA* STUDIED IN OREGON.

Name	Region	Location	Species	Type
Fulton Farm	Columbia River Gorge	S. side of Dalles bridge on Fulton Farm	*A. speciosa, A. fascicularis*	mixed
Mosier A	Columbia River Gorge	Mosier exit along scenic Hwy	*A. speciosa, A. fascicularis*	mixed
Mosier B	Columbia River Gorge	Mosier exit along scenic Hwy	*A. fascicularis*	unispecific
Memaloose	Columbia River Gorge	Memaloose State Park	*A. fascicularis*	unispecific
Brooklane	Willamette Valley	Brooklane Rd in Corvallis	*A. fascicularis*	unispecific
Mistletoe	Willamette Valley	W. side of Hwy 99, milepost 78	*A. speciosa*	unispecific
Perrydale-Bethel	Willamette Valley	On Bethel Rd in Perrydale	*A. speciosa*	unispecific
Rickreal	Willamette Valley	NW corner of Hwy 99 and Hwy 22 at Rickreall; 10 mi E of Salem	*A. speciosa*	unispecific
Wilson A	Willamette Valley	Hwy 99 at EE Wilson Wildlife Refuge	*A. speciosa*	unispecific

Flowering and fruiting phenology. We quantified reproduction in both co-occurring and mixed populations of *A. speciosa* and *A. fascicularis* to determine if flowering overlap was sufficient to allow pollen exchange between the two species. Observations in all localities began in late May and continued for nine weeks through the end of July. We monitored flowering phenology weekly on 20 ramets that were selected haphazardly in each population and grew at least one meter from other marked stems. We used stratified sampling in large populations, and ramets less than ten centimeters apart were considered to be part of the same genet. To evaluate flowering times among species, we counted and compared the number of flowering umbels/ramet (i.e., those with at least one open flower). Fruits were produced and gathered from late July to September.

FIG. 1. Paired pollinia of *A. fascicularis* and *A. speciosa* attached by their translator arms to a grooved corpusculum. The maximum length and width measures are denoted on a pollinium of *A. speciosa*. Drawing by Felicia Russell.

Ethological barriers: insect observations. We observed insect visitors to determine if individual insects fly between the two species of milkweed and if the same insect taxa visit and pollinate both *A. speciosa* and *A. fascicularis*. Insect observation plots were located randomly in the populations and were uniformly 1×1 meter in area. Visitors to both *A. speciosa* and *A. fascicularis* were monitored from mid June until the end of July, primarily in mixed populations. For each standard observation period of 10 minutes (Kearns and Inouye 1993; Dafni and Kevan in press), we recorded the insect morphotype and the duration of visits to umbels and ramets. Most insects were identified to genus or family within each order from vouchers collected on site, and deposited at Willamette University.

Mechanical barriers: pollinia and stigmatic chamber measurements. The sizes of pollinia and stigmatic chambers of *A. speciosa* and *A. fascicularis* were compared to determine if it is mechanically possible for the two species to hybridize. To measure the pollinia from both species, random samples of 15 or more flowers were collected from each population. One pollinarium was removed from each flower, placed on a micrometer slide (0–2 mm) under a compound microscope and measured for the length of the corpusculum and the maximum length and width of each pollinium (Fig. 1). We measured the maximum internal length and width of the stigmatic chamber by removing the wings and placing them flat on a micrometer slide.

Experimental test crosses. Experimental crosses were carried out in the field to test if pollen exchange between *A. speciosa* and *A. fascicularis* would produce fruit. The number of intraspecific crosses (controls) as well as reciprocal interspecific crosses depended on the size and availability of plants in a given population, but these included over 80 pollinations in all possible combinations. In addition to intraspecific cross-pollinations, inter-

specific crosses were made in the two mixed populations and in several single species populations. To exclude pollinators and other insects, each umbel was covered with fine mesh while flowers were still in bud. Once flowers opened in bagged umbels, one to three pollinations per umbel were performed with only one insertion per flower. This required removing pollinia from the maternal plant and inserting pollinia from a nearby paternal donor at the correct angle without damaging the stigmatic chamber. Plants were then re-bagged until fruit production. Later, we counted the number of fruits and seeds produced to determine the success of the interspecific and intraspecific crosses.
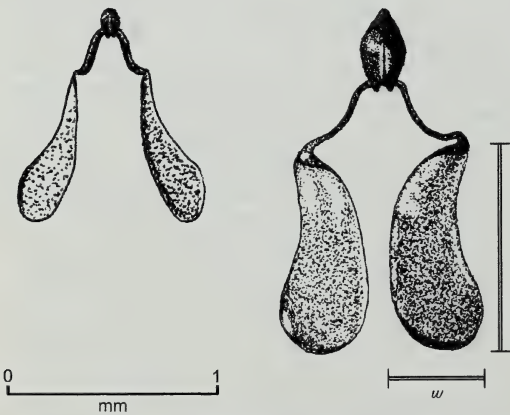
Germination study: viability of hybrid offspring. For a pilot study of hybrid viability relative to parental types, we collected seeds from successful field crosses between A. *fascicularis* and A. *speciosa* and from intraspecific pollinations of A. *speciosa* and A. *fascicularis.* The hybrid seeds represented progeny from crosses made within four different field populations. We sowed 36 seeds in 7.62 cm^2 pots filled with equal amounts of potting soil and monitored germination and seedling growth for each seed type every three days. The seeds were not cold-stratified or nicked since seeds of parental species were previously germinated successfully in the glasshouse for botanical use without pre-treatment. Height was measured once the embryonic stem was visible above soil level; the germination and growth of the hybrid offspring could therefore be determined relative to that of non-hybrid seeds and seedlings.

To further evaluate the relative fitness of the hybrids, we measured the size and number of seeds produced from fruits that resulted from hybrid and intraspecific field pollinations. Because the Levine test indicated that variances were not homogeneous, we used non-parametric statistical tests (Kruskal-Wallis, Mann-Whitney) to determine if hybrid seeds and fruits differed from those produced after intraspecific matings.

Species distinctions and evidence of character displacement. Confirmation of species distinctions and evidence of character displacement within milkweed populations were investigated by comparison of morphological traits in co-occurring and unispecific populations of the two species. Vegetative and reproductive structures were collected from at least 15 randomly chosen plants in each population and measured for 11 characters. In addition to the floral and seed traits described earlier, we measured leaf length and maximum width, floral hood depth and maximum width, number of ramets/plant, and number of umbels/ramet. Hoods were measured by removing one hood for stabilization, then electronically scanning the flower along with a mm scale. We used *t*-tests or non-parametric methods, as appropriate, to compare the two species.

To evaluate the similarity of characters among species and among populations in different geographic regions, we conducted two types of multivariate Principal Component Analyses (PCA-SPSS): in the first, all reproductive characters and individuals (OTU's) were entered. However, we wanted to minimize the effect of size differences in the development of clusters generated from principal component scores; thus, prior to inclusion in taxon matrices, we standardized all characters using the mean and standard deviation for each species (Sneath and Sokal 1973). A second analysis was used to explore the possibility that character differences between species were exaggerated in mixed populations. In this analysis, individual population means (OTU's) were computed separately for each co-occurring and mixed population of a species, and compared graphically relative to the overall mean of the congeneric species. Character displacement would be detected if distances between mixed populations and the congeneric mean were greater than those for unispecific populations, as a result of selection against hybridization or to reduce competition.

RESULTS

Flowering time. Temporal variation in the onset of floral initiation was common, along with some overlap in flowering time between populations of the two species. However, unispecific populations of A. *fascicularis* showed greater flowering overlap with A. *speciosa* in all geographic regions than did sympatric populations of A. *fascicularis* (Fig. 2). Flower initiation was earliest for Columbia Gorge populations of A. *speciosa,* with a peak in mid-June to early July. Co-occurring populations of A. *fascicularis* in the same area did not initiate flowering until early July. Although flowering was not studied quantitatively at all sites for A. *fascicularis,* Willamette Valley populations flowered in July and August, usually later than Willamette Valley populations of A. *speciosa.*

Ethological barriers: insect observations. Mixed and isolated populations were readily available in the Columbia River Gorge for monitoring insect visitation to A. *speciosa* and A. *fascicularis.* Honeybees (*Apis mellifera*) predominated in all study populations, and visitation levels on the two milkweed species were indistinguishable where plants co-occurred at Mosier A (Fig. 3). In contrast, bumblebees (*Bombus* sp.) were prevalent in addition to *Apis* on plants in unispecific populations of A. *fascicularis* at Mosier B. Although plants grew near one another in mixed populations, insects did not fly between them during timed observation intervals in 2001. In the Columbia River Gorge, Kephart has observed flights between these species by native bees and wasps, but not honeybees. The highest insect diversity occurred at Fulton Farm on A. *speciosa* (Fig. 3), but this may reflect more exten-
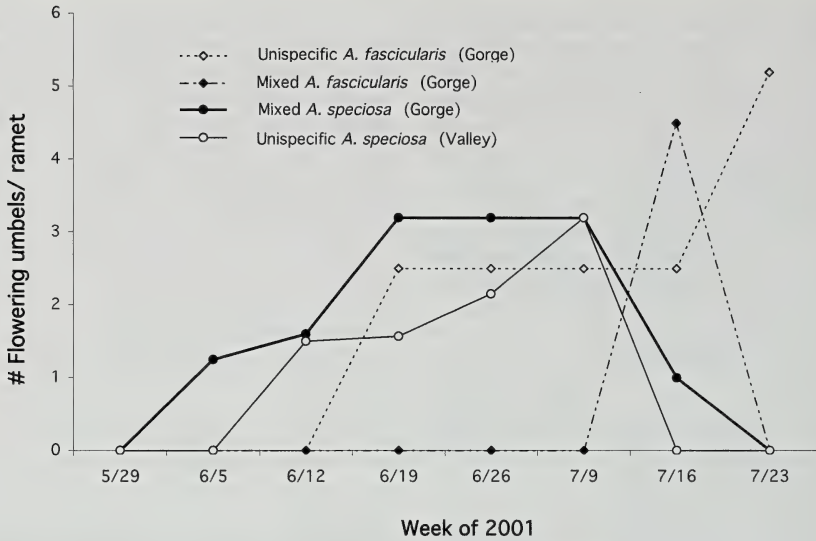
FIG. 2. Flowering phenology of unispecific and mixed populations of *Asclepias*.

sive observations during the long period of peak flowering of *A. speciosa* at this site.

Mechanical barriers: pollinia and stigmatic chamber measurements. Measurements of pollinium length and width, corpusculum length, and stigmatic chamber length and width differed significantly between species, and were largest for *A. speciosa* (Mann-Whitney U-Test, $P < 0.01$; Fig. 4).

Experimental test crosses. Overall, interspecific crosses performed in the field averaged 14.5 per-

cent fruit-set, compared to means of 13 and 15% fruit-set for intraspecific pollinations within *A. fascicularis* and *A. speciosa,* respectively. Surprisingly, the most successful pollinations were *interspecific* crosses with *A. speciosa* as the paternal donor (35% fruit-set; Table 2). In contrast, no fruits resulted from interspecific crosses with *A. fascicularis* as paternal donor. Pollination success also varied among populations, ranging as high as 33% for intraspecific pollinations at Wilson and 50% for interspecific crosses at Memaloose.
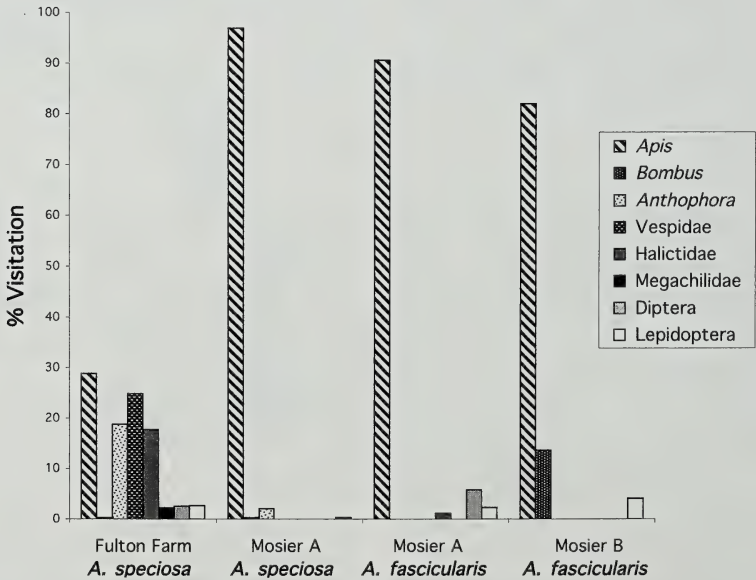
FIG. 3. Proportions of visits by insect taxa to flowering umbels within sympatric populations of *A. speciosa* and *A. fascicularis.*
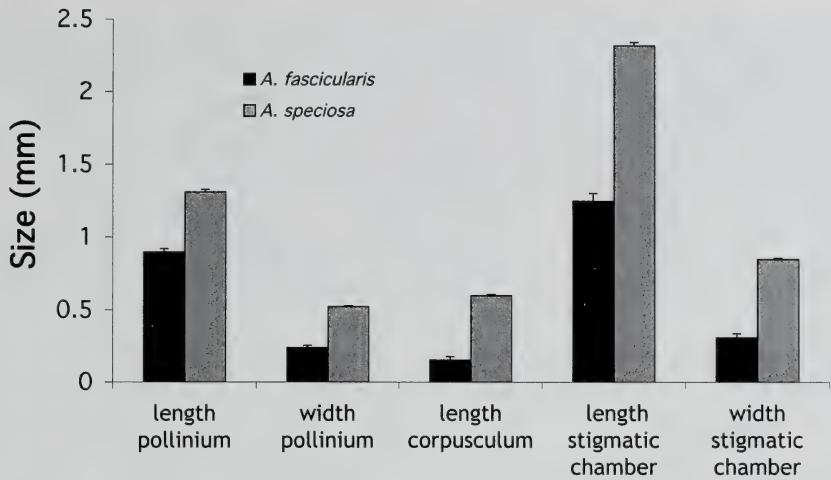
Floral Structure

Fig. 4. Mean sizes and standard errors of floral structures in *A. speciosa* and *A. fascicularis*; estimates the potential for mechanical barriers to hybridization.

Germination study: viability of hybrid offspring. Seed size varied significantly among parental taxa and hybrids for both length and width (Kruskal-Wallis and Mann-Whitney tests, $P < 0.001$; Table 3). Hybrid seeds were intermediate in width between the larger *speciosa* and smaller *fascicularis* seeds, but closer in length to the maternal parent, *A. fascicularis* (Table 3). The number of hybrid seeds produced in fruits on *A. fascicularis* was also comparable to its seed number after intraspecific pollination (Table 3). Fruits with hybrid seeds were smaller than fruits of intraspecific crosses with either parent (Mann-Whitney U-test, $P < 0.05$; Table 3).

Despite a presumed lack of seed dormancy, germination was low for both hybrid and parental seeds in the pilot study. Seed germination was equivalent for hybrids and *A. speciosa* (17% success), but seedling growth (Fig. 5) and mean seedling height at 21 days were greater for *A. speciosa* (27.5 ± 2.5 mm, SE) than for hybrids (21.5 ± 0.5 mm). *A. fascicularis* seeds had fungal contamination and did not germinate, but undetected dormancy and insufficient after-ripening may have further influenced their germination.

Species distinctions and evidence of character displacement. *A. speciosa* and *A. fascicularis* differed significantly for 11 vegetative and reproductive characters (Mann-Whitney Test, $P < 0.01$). In addition, they differed in aspects such as leaf pubescence, umbel structure, and flower coloration that were not measured. In a PCA analysis of all reproductive characters, slight differentiation exists within species among Columbia River Gorge versus Willamette Valley populations (Fig. 6). Although we standardized matrix elements by species means to minimize the evident size differences among taxa, the OTU's of *A. fascicularis* populations form a cohesive cluster at the extreme of the range observed for *A. speciosa*. The first principal component explained 54.9% of the variation in the data. Plots of principal component scores using population means do not provide clear evidence for character displacement of either species away from its congener in mixed populations (Figs. 7A, B). The first principal components for runs involving *A. fascicularis* and *A. speciosa* explained 55.5 and 54.9% of the variance, respectively. For *A. speciosa*, only hood length of flowers was greater in mixed than unispecific populations. For *A. fascicularis* populations, hood depth, pollinium length and corpusculum length were slightly smaller in sites where plants co-occurred with *A. speciosa*.

TABLE 2. PERCENT FRUIT PRODUCTION FOR INTRASPECIFIC AND INTERSPECIFIC POLLINATIONS OF *A. FASCICULARIS* AND *A. SPECIOSA*. N is the number of pollinia successfully inserted into stigmatic chambers. For populations with fruit-set, we show the percentage range of insertions resulting in fruits.

Maternal parent	Paternal donor	N	% Fruit-set	Range
Interspecific Crosses				
A. fascicularis	A. speciosa	23	34.7	20–50
A. speciosa	A. fascicularis	32	0	0
Intraspecific Crosses				
A. speciosa	A. speciosa	20	15.0	16–33
A. fascicularis	A. fascicularis	8	12.5	12.5

TABLE 3. MEANS AND STANDARD ERRORS OF SEED CHARACTERS FOR *A. FASCICULARIS, A. SPECIOSA* AND HYBRIDS FOLLOW-ING INTRASPECIFIC AND INTERSPECIFIC POLLINATION. Hybrid seeds are from pollinations in which *A. fascicularis* was the maternal parent. Differing superscripts within characters indicate significant differences (Kruskal-Wallis test among species; and hybrids; Mann-Whitney U-test was employed for pair-wise comparisons: for fruit length $P = 0.03–0.05$, for seed characters $P < 0.001$).

Character	N	*A. fascicularis*	Hybrids	*A. speciosa*
Seed length (mm)	60–120	6.5[a] ± 0.05	6.9[b] ± 0.05	7.6[c] ± 0.08
Seed width (mm)	60–120	2.8[a] ± 0.04	3.7[b] ± 0.04	4.6[c] ± 0.06
Seed number/fruit	6–12	35.6[a] ± 2.1	33.0[a] ± 4.5	161.5[b] ± 14.4
Fruit length (mm)	6–12	73.8[a] ± 3.4	61.9[b] ± 1.9	84.3[c] ± 6.9

However, these differences between unispecific and mixed populations were not statistically significant.

DISCUSSION

Whether one regards speciation as a process primarily originating in sympatry or allopatry, some form of spatial or ecological isolation is strongly implicated in species divergence, and may be reinforced by other reproductive barriers (Charlesworth 1995; Arnold 1997; Schemske 2000). In *A. speciosa* and *A. fascicularis*, both pre-mating and post-pollination mechanisms were effective in reducing or preventing the exchange of pollen and the formation of hybrid offspring. Both species were visited freely by a variety of polylectic bees, but the earlier flowering of *A. speciosa* in sympatric populations and its significantly larger pollinia and stigmatic chambers likely limit pollinium transfer to *A. fascicularis*. In fact such artificial crosses were quite difficult; anther wings had to be spread to accommodate the larger pollinia. Similarly, in sympatric populations of three midwestern *Asclepias,* a one-way mechanical barrier prevented insertion of large *A. syriaca* pollinia into the stigmatic chambers of two small-flowered species (Kephart and Heiser 1980). Broyles et al. (1996) also suggest that the large pollinia of *A. syriaca* occur less often than predicted in smaller *A. exaltata* flowers.

In contrast, in reciprocal crosses with *A. fascicularis* as the paternal parent, small pollinia were easily inserted into stigmatic chambers of *A. speciosa* but did not form fruit. Ovule number is large in *A. speciosa,* so a single pollinium of *A. fascicularis* might not supply enough pollen grains to prevent fruit abortion (Bookman 1984), but we did not detect fruit initiation, which suggests a different explanation. Other possibilities include poor pollen germinability, genetic incompatibility, or that pollen tubes are too short to reach the ovules of *A. speciosa* (Kephart 1981; Kahn and Morse 1991; Lipow and Wyatt 2000). Also, despite magnification, pollinia are difficult to insert effectively in the field in variable weather, a factor that may have reduced the success of all pollination types.

An interesting and unexpected result was the modest success of within species pollinations rela-
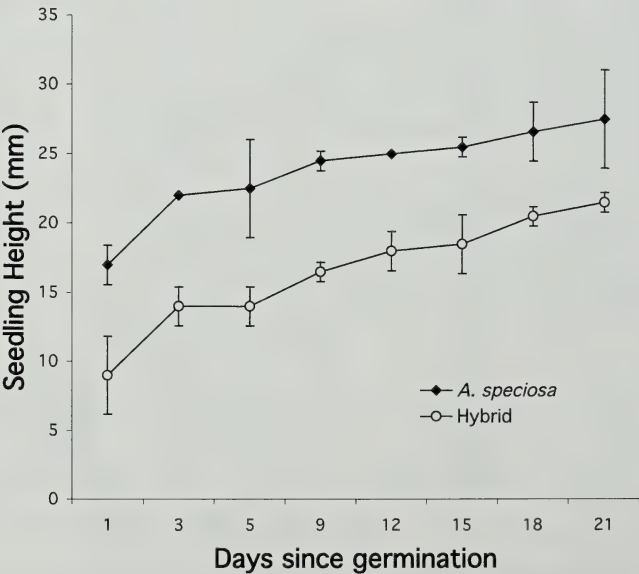
FIG. 5. Growth of seedlings derived from hybrid crosses and intraspecific pollinations within *A. speciosa*.

PCA Morphology by Population Location
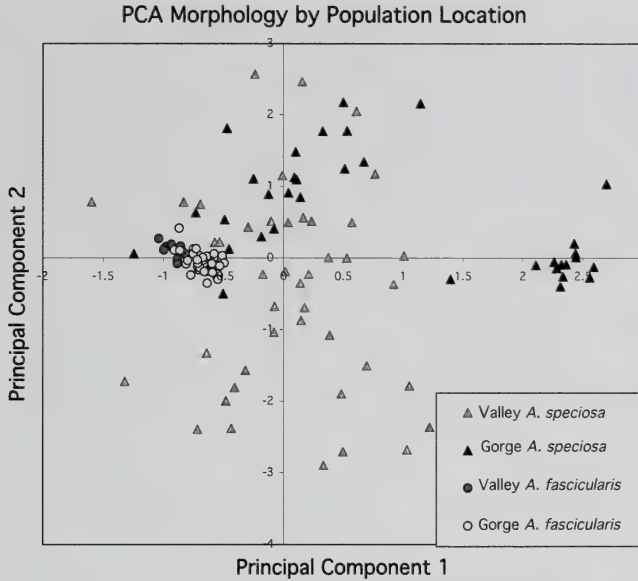
Fig. 6. Two-dimensional scatter-plot of first and second principal component scores after PCA of morphological characters for individuals (OTU's) for Columbia River Gorge and Willamette Valley populations.

tive to the much higher fruit-set in interspecific crosses with small-flowered *A. fascicularis* as the maternal parent. This unusual finding suggests that as a paternal donor, *A. speciosa* easily forms pollen tubes of adequate length to reach ovules of *A. fascicularis*. Thus, their vigor, number, or genetic makeup improved the probability of fruiting relative to conspecific *A. fascicularis* pollen, and are factors worth exploring in future studies. For example, pollen tubes of *A. speciosa* might have greater size-induced vigor, making it more likely for these to reach the ovules successfully. A similar size advantage was also postulated for larger pollinia of *A. syriaca* relative to hybrid formation with *A. exaltata* (Wyatt and Broyles 1992). Second, because most asclepiads show partial or complete self-incompatibility (Broyles and Wyatt 1993; Lipow and Wyatt 2000), inbreeding or low genetic diversity may render conspecific pollinations less effective than expected in both species despite attempts to use pollinia from different genets. Insufficient compatible genotypes often exist in small, clonal populations (e.g., *Hymenoxys acaulis*; De Mauro 1993), and are very possible in *Asclepias* given the small, highly fragmented populations remaining in Oregon, and the clonality of many species including *A. speciosa* (Bookman 1984).

Discussions of the relative roles of mechanical and physiological barriers in maintaining species boundaries in *Asclepias* date back many years (e.g., Grant 1949; Woodson 1954), and this study further underscores the importance of examining reproductive isolation from both ecological and genetic perspectives. Greenhouse germination studies demonstrated that the exchange of pollen between *A. speciosa* and *A. fascicularis* can produce viable hybrid offspring of equal germination capability and but reduced stature, even if the event is probably infrequent in nature. It is interesting that for species combinations for which the insertion of pollinia is difficult to impossible in nature (*A. speciosa* into *A. fascicularis* chambers), post-mating barriers are absent, whereas for the easier reciprocal insertion, genetic or physiological mechanisms prevent fertilization and/or fruit-set. We still know comparatively little, however, about the fitness of hybrids of reproductive age, or the relative fitness of *A. fascicularis* seedlings. The lack of germination in *A. fascicularis* seeds presumably reflects either genetic incompatibilities among parents, insufficient maturation of these later-developing fruits, or the higher incidence of fungal contamination of these seeds in the greenhouse.

The strong pre-mating and post-mating barriers to hybridization, and the evident morphological differentiation, confirm that *A. speciosa* or *A. fascicularis* are well-delineated from one another as taxonomic species. Both species occur in different series of the genus *Asclepias* (Incarnatae for *A. fascicularis*; Purpurascentes for *A. speciosa*) and appear unlikely to share genes through hybridization. If these species were once allopatric, divergence may have arisen independent of any contact between them, and the reproductive isolation between them may be a simple by-product of adaptive divergence at genetic loci that are pleiotropic or linked to those conferring isolation (Fitzpatrick 2002). We also asked whether selection against hybridization or competition might have occurred, manifesting itself in greater character displacement

A   PCA--*A. fascicularis* Populations

B   PCA--*A. speciosa* Populations
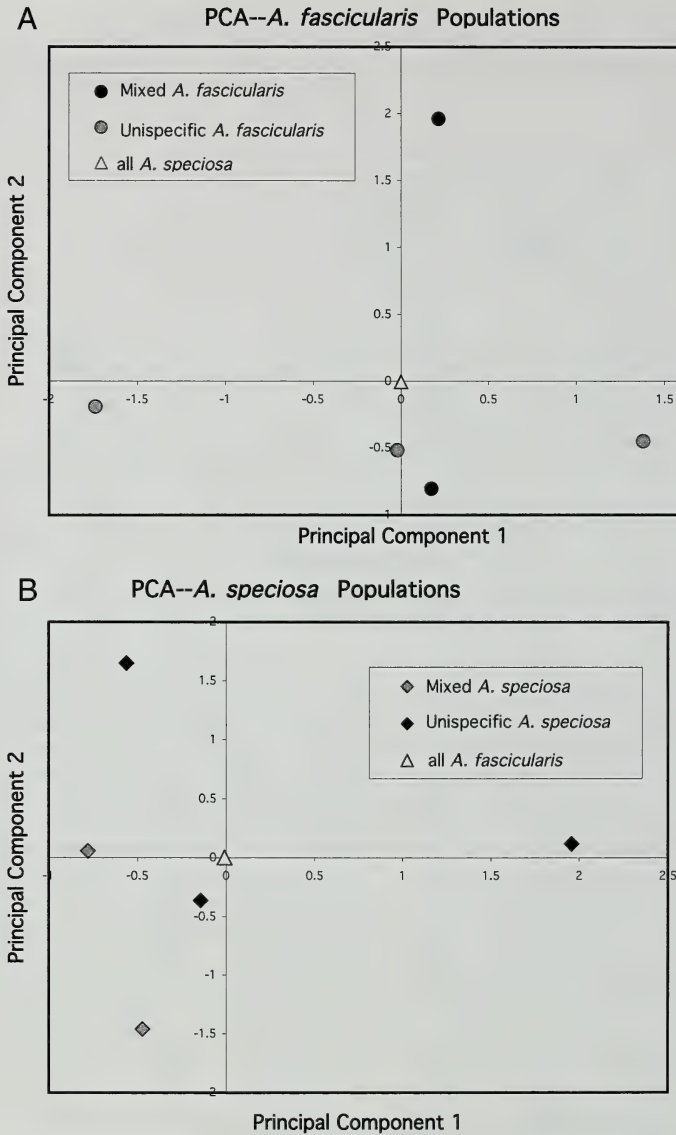
FIG. 7.   Two-dimensional scatterplot of first and second principal component scores after PCA based on OTU's for population means of: **(A)** unispecific and mixed *A. fascicularis* (Table 1) relative to mean for all *A. speciosa* populations. **(B)** unispecific and mixed populations of *A. speciosa* relative to mean for all *A. fascicularis* populations.

in sympatric populations. For instance, two central Mexican species, *Solanum grayi* and *S. tumholtzianum* are similar in floral size in their respective ranges, but diverge in areas where they co-occur (Whalen 1978). In these taxa, and similarly related species of *Fuchsia* and *Phlox,* the divergent floral sizes or colors within zones of sympatry allow plants to exploit different pollinators, reducing the likelihood of pollen exchange (Breedlove 1969; Levin 1985; Judd et al. 1999). In contrast, we detected no significant differences in the sizes of reproductive characters in co-occurring versus isolat-

ed populations of *A. speciosa* or *A. fascicularis* that would suggest directional selection away from a congener nor isolation via differing pollinators. Temporal factors may also potentially reduce gene flow between species as we detected some divergence in flowering time for *A. fascicularis* in mixed populations. Overall, the extent to which insect visitors and flowering times differ or overlap across the ranges of the two species merits more extensive study in relation to reproductive isolation. Pollinator abundances vary spatially and temporally, and even plants with specialized reproductive structures

may retain characters that attract a generalized array of visitors (Waser 1998).

Understanding the frequency and nature of hybridization in a genus can clarify the history and diversity of particular species (Milne 1999), and help build general paradigms in model study systems (e.g., Hodges and Arnold 1994; Wolfe et al. 1998; Rieseberg 2000). Reproductive barriers in *Asclepias* suggest a pattern worth exploring in future studies. For example, post-mating barriers appear less evident in species pairs with strong spatial or ecological isolation. Thus, pre-mating barriers prevail between geographically allopatric, but ecologically similar *A. speciosa* and *A. syriaca,* and among sympatric populations of *A. exaltata* and *A. syriaca,* which differ ecologically in both flowering time and habitat type (Kephart et al. 1988). After human disturbance, or during succession, hybrid swarms or zones are possible in which hybrids or introgressants may have a selective advantage over parental species (Kephart et al. 1988; Wyatt and Broyles 1994). In contrast, for species that are both geographically and ecologically sympatric, post-mating isolation occurs and hybridization seems non-existent. In western *A. speciosa* and *A. fascicularis,* these barriers occurred in the crossing direction least protected by pre-mating factors. Post-mating factors also reinforce pre-mating isolation and prevent hybridization among sympatric species *A. verticillata* and *A. incarnata*: although these species grow in soils of varying moisture levels, they co-occur in open prairies where these habitats closely intermingle (Curtis 1955; Kephart and Heiser 1980).

Previous studies have shown that particular hybrid offspring can be favored by selection as part of adaptive evolution (Rieseberg 1998). Natural hybridization was not observed in co-occurring western milkweeds, but additional exploration of the extent and genetic basis of pre-mating and post-mating reproductive isolation should enhance our understanding of the evolution of asclepiads and other plant species.

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GENETIC DIVERSITY IN THE RARE, INSULAR ENDEMIC
SIBARA FILIFOLIA (BRASSICACEAE)

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Abstract

This study investigates genetic variation in the rare insular endemic *Sibara filifolia*, a species consisting of few, small, narrowly-distributed populations. Electrophoretic data for 29 allozyme loci were obtained for individuals collected as seed from the three known populations on San Clemente Island. Overall levels of genetic variation are low. Only two polymorphic loci were observed, resulting in low number of alleles per locus (1.01), average observed heterozygosity (0.006) and average expected heterozygosity (0.009) for populations. Interestingly, all polymorphism occurred in just one of the three populations, in spite of their close proximity. Most variation on San Clemente Island is thus found within rather than among populations ($G_{ST} = 0.144$), and there is significant differentiation among populations ($F_{ST} = 0.145$). Gene flow is estimated as Nm = 0.41 based on private alleles and Nm = 1.49 based on F_{ST}. The differentiation of populations and low level of gene flow suggests that genetic drift is a potent force in these small populations and may further reduce genetic variation. RAPD and quantitative genetic studies are recommended to further evaluate these populations and the long-term prospects for this species.

Key Words: Allozymes, conservation, *Sibara*, endangered species, endemic, genetic diversity, Brassicaceae, San Clemente Island.

The genetic characteristics of rare species have commanded considerable attention in the last few decades. Genetic variation is understood to be important to the continued survival of organisms, both in the long-term (through ability to adapt to a changing environment; Holsinger and Gottlieb 1991; Ellstrand and Elam 1993) and in the short-term (through increased fitness in spatially or temporally heterogeneous environments, by reducing inbreeding, and by other mechanisms; Huenneke 1991). In general, rare species are assumed to be more vulnerable to extinction because of reduced genetic variation, in addition to habitat and demographic factors.

Rabinowitz (1981) pointed out that rarity can be subdivided into three separate components: a species can be considered rare due to small geographic range, high habitat specificity, or small population size (or combinations of these factors). Reduced genetic variation is associated with all three of these factors. Narrow-ranging species generally contain less genetic diversity than wide-ranging species, both at the population and species levels (Hamrick and Godt 1989; Gitzendanner and Soltis 2000), presumably because of isolation of populations or diversifying selective forces across the species range (Baskauf et al. 1994). Strong directional selection leading to genetic uniformity in a limited array of environments and genetic drift in small populations are expected to cause depleted levels of genetic variation (Wright 1931; Babbel and Selander 1974; Nei et al. 1975; Franklin 1980; Barrett and Kohn 1991). A species exhibiting rarity in all three of these components would be predicted to have very low levels of genetic variation.

This study investigates the genetic variation in the rare insular endemic *Sibara filifolia*, a species consisting of few, small, narrowly-distributed populations, and appearing to demonstrate habitat specificity. The specific goals were to (1) assess the genetic diversity remaining in this geographically highly restricted species, (2) evaluate the distinctness of the populations, and (3) provide management guidelines based on population genetic data. This study was initiated as part of an investigation of the conservation genetics of rare and endangered plant species of San Clemente Island.

Materials and Methods

Study Species

Sibara filifolia (E. Greene) E. Greene (Brassicaceae), the Santa Cruz Island Rockcress, is a diminutive annual apparently restricted to rocky outcrops. First described from Santa Cruz Island in 1886 (Greene 1887), it was last seen there in 1936 and was not relocated during a survey of the island in 1985. Trask reported it from two locations on Santa Catalina Island in 1901 (Thorne 1967); it was last seen on that island in 1973 and was not relocated during a survey in 1996. The species was presumed extinct until two individuals were located on a sea terrace at the southern end of San Clemente Island in 1986, growing on volcanic rock scree (Beauchamp 1987); it was given federal endangered status in November 1997. Until June 2001, *S. filifolia* was known only from populations on three adjacent ridges within 150 m of each other on San Clemente Island and from occasional scattered individuals nearby; a few individuals have
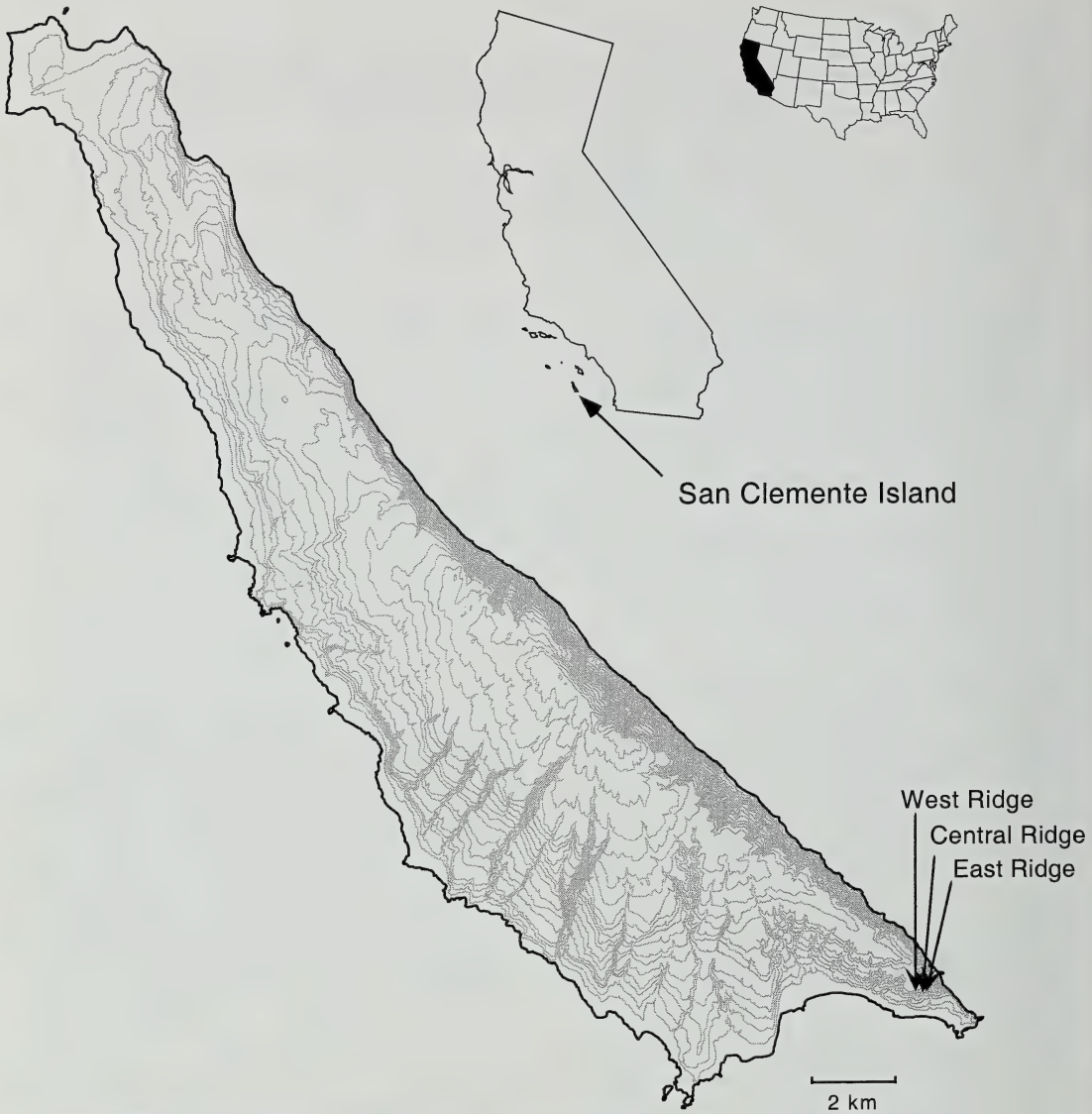
FIG. 1.   Sampled populations of *Sibara filifolia* on San Clemente Island.

now been relocated on Santa Catalina Island (G. Wallace, USFWS, personal communication).

Sampling

A single fruit was collected from each individual bearing more than three fruits from the three known locations in June 1996 (Fig. 1). Seeds were sown in the greenhouse and leaf tissue was collected from one progeny from each parent. Sample sizes were 16 (West Ridge), 13 (Central Ridge), and 22 (East Ridge), for a total of 51 individuals; sample size was limited by availability of larger plants and by seed viability and germination.

Electrophoresis

Electrophoretic methods followed Soltis et al. (1983). Leaf tissue was crushed in phosphate extraction buffer (Conkle et al. 1982) and stored at $-80°C$ until electrophoresis was conducted.

Three buffer systems were used to resolve loci coding for 18 enzymes. Acid phosphatase (Acp), isocitrate dehydrogenase (Idh), and phosphogluconate dehydrogenase (Pgd) were resolved using a tris-citrate, pH 6.3/6.7 buffer system (Selander et al. 1971) with 11.5% starch gels. Aldolase (Ald), diaphorase (Dia), fructose-1,6-diphosphatase (Fdp), glucose-6-phosphate dehydrogenase (G6p), leucine

aminopeptidase (Lap), malate dehydrogenase (Mdh), malic enzyme (Me), menadione reductase (Mr), phosphoglucoisomerase (Pgi), and superoxide dismutase (Sod) were resolved using a morpholine citrate, pH 6.1 buffer system (Clayton and Tretiak 1972) with 13% starch gels. Glutamate dehydrogenase (Gdh), glyceraldehyde-3-phosphate dehydrogenase (G3p), phosphoglucomutase (Pgm), shikimate dehydrogenase (Skd), and triose-phosphate isomerase (Tpi) were resolved with using a tris-borate-EDTA, pH 8.6 buffer system (Soltis et al. 1983) with 11% starch gels.

Staining recipes for all enzymes followed Soltis et al. (1983), except for Dia and Sod (Murphy et al. 1990). Loci were numbered sequentially with the most anodally migrating enzyme designated "1".

Data Analysis

Data were analyzed using the computer program Genestrut (Constantine et al. 1994). Mean number of alleles per locus (A), effective number of alleles (A_E), percentage of polymorphic loci (P), observed heterozygosity (H_O), and expected heterozygosity (H_E) were calculated. Loci were considered polymorphic if more than one allele was detected. Levels of genetic variation were calculated for individual populations, and also for the entire species on San Clemente Island. Fixation indices (F), reflecting deviations from Hardy-Weinberg equilibrium, were calculated and outcrossing rates (t) were estimated using $t = (1-F)/(1+F)$ (Weir 1990).

The partitioning of genetic diversity within and among all populations was analyzed using F-statistics (Nei 1973). Nei's (1978) unbiased genetic identity (I) was calculated for pairwise comparisons of populations using Genestrut (Constantine et al. 1994).

Gene flow was estimated using Wright's (1951) formula $Nm = (1 - F_{ST})/4F_{ST}$, with F_{ST} considered equivalent to G_{ST} (Nei 1977). A second estimate was based on the frequency of private alleles (alleles found in a single population; Slatkin 1985).

RESULTS

Loci and Alleles Scored

Enzyme electrophoresis resulted in clear and consistent staining for 18 enzymes encoded by 29 putative loci: Acp, Ald, Dia, Fdp-1, Fdp-2, Gdh, G3p-1, G3p-2, G3p-3, G6p-1, G6p-2, Idh, Lap, Mdh-1, Mdh-2, Mdh-3, Me, Mr-1, Mr-2, Pgd, Pgi-1, Pgi-2, Pgm-1, Pgm-2, Skd, Sod-1, Sod-2, Tpi-1, and Tpi-2. All enzymes migrated anodally.

A total of 32 alleles were detected for the 29 loci. All loci except Mdh-2 and Pgi-2 were monomorphic with all individuals from all populations possessing a single enzyme band with identical mobility for each locus. Mdh-2 had two alternative alleles (found at frequencies of 0.03 and 0.22), and Pgi-2 had one variant allele (at a frequency of

TABLE 1. GENETIC VARIABILITY AT 19 LOCI IN 3 POPULATIONS OF *SIBARA FILIFOLIA*.

Population	A	A_E	P	H_O	H_E
West Ridge	1.10	1.03	6.9	0.017	0.027
Central Ridge	1.00	1.00	0.0	0.000	0.000
East Ridge	1.00	1.00	0.0	0.000	0.000
Mean	1.03	1.01	2.3	0.006	0.009
(SE)	(0.03)	(0.01)	(2.3)	(0.006)	(0.009)
Species	1.10	1.01	6.9	0.005	0.010

0.25); all of these occurred only in West Ridge. Average frequency of alternative alleles is 0.17. Heterozygotes were observed for both alleles at Mdh-2, but no heterozygotes were observed for Pgi-2.

Measures of Genetic Variability

At the species level, *S. filifolia* has low levels of genetic variation, with 6.9% polymorphic loci and low heterozygosities (Table 1). Two of the three populations (Central Ridge and East Ridge) are monomorphic at all loci; genetic variation was only observed in West Ridge, and even this population is low in allozyme variation.

Genetic Identity Measures

Genetic identity values (I; Nei 1978) are very high. Central Ridge and East Ridge populations, being monomorphic and identical, have a genetic identity of 1.000. West Ridge has a genetic identity of 0.997 with the other two populations (mean I = 0.999).

Fixation Indices and Outcrossing Rates

Of the two fixation indices (F; available only for Mdh-2 and Pgi-2 in the West Ridge population), one was non-significant (Mdh-2; F = −0.292; ns) and the other was significant and positive (Pgi-2; F = 1.000; P < 0.01), indicating a deficiency of heterozygotes (mean F = 0.754).

The outcrossing rate based on the mean fixation index is t = 0.457, indicating a significant level of inbreeding (t = 0 for complete self-fertilization and t = 1 for random mating).

F-statistics

Mean F_{IS}, representing average deviation from Hardy-Weinberg expectations within populations, is significant for *S. filifolia* on San Clemente Island (mean F_{IS} = 0.373, P < 0.01). Differentiation of populations is evident and significantly different from 0 (mean F_{ST} = 0.145, P < 0.01). Of the total gene diversity found on San Clemente Island, 85.6% is found within populations and 14.4% is found among populations (mean H_S = 0.133, mean D_{ST} = 0.022, mean H_T = 0.155, G_{ST} = 0.144).

Gene Flow

Gene flow among populations was Nm = 0.41 using Slatkin's (1985) method based on 3 private alleles with an average frequency of 0.167 and corrected for an average population size of 17. Wright's (1951) method yielded an estimate of Nm = 1.49.

DISCUSSION

Genetic Variation

The low level of genetic variation observed in *S. filifolia* conforms to expectations for a narrowly-distributed taxon consisting of few, small populations. These data agree with empirical observations of many other plant species with a restricted range (Hamrick and Godt 1989; Gitzendanner and Soltis 2000). In addition, insular endemic plants generally appear to have lower levels of genetic variation, even within populations, presumably due to a history of founder events and population bottlenecks (DeJoode and Wendel 1992; Frankham 1997), although studies of other Channel Islands' endemics have revealed a range of levels of genetic variation (Helenurm 2001; Dodd and Helenurm 2002). *Sibara filifolia* also possesses other attributes associated with lower levels of genetic variation, such as production of seeds without pollinators (see below) and gravity-dispersed seeds (Hamrick and Godt 1989).

Recent ecological history is also likely to have affected levels of genetic variation in *S. filifolia*. Grazing pressure by introduced livestock (primarily goats) kept populations of most native species small during the last century (Kellogg and Kellogg 1994). Small populations are vulnerable to genetic drift, and especially to the rapid loss of rare alleles. Population sizes of *S. filifolia* are likely to have been extremely small, as it remained undiscovered by botanists until 1986. It is likely that many rare alleles have been lost in populations, resulting in a genetically depauperate species. Even after removal of goats in 1992 (Kellogg and Kellogg 1994), population sizes of this annual plant have often been small and fluctuated widely (Junak and Wilken 1998; K. Helenurm personal observation), reducing effective population size. Moreover, the original range of *S. filifolia* on San Clemente Island is not known, and may have been considerably larger than at present; range restriction may also have resulted in a loss of genetic variation. Although the seed bank may harbor additional genetic variation not observed in this study, the 51 plants surveyed represent a large enough sample to conclude that genetic variation in *S. filifolia* is low in comparison to most plant species.

Genetic Differentiation

A surprising result of this study is the significant differentiation of populations in spite of their close proximity. Two populations (Central Ridge and East Ridge, separated by 50 m) are completely monomorphic at 29 loci, while the third (West Ridge, only 100 m distant from Central Ridge), contains additional alleles at substantial frequencies at two loci. Although one of the Mdh alleles is rare (Mdh-2a, at a frequency of 0.03), the other is more common (Mdh-2c, at a frequency of 0.22) for a combined alternative allele frequency of 0.25; Pgi-2a occurs at a frequency of 0.25. This suggests that very little gene flow occurs in *S. filifolia*, even over short distances; quantitative estimates of gene flow from the electrophoretic data are Nm = 1.49 based on differentiation at polymorphic loci (Wright 1951) and Nm = 0.41 based on private alleles (Slatkin 1985). While the accuracy of these estimates is questionable due to the detection of only two polymorphic loci and three private alleles, they nevertheless summarize the available genetic data, and both indicate little gene flow based on different methods of estimation.

The significant differentiation of populations at allozyme loci and inference of low gene flow is consistent with greenhouse observations of the breeding system of *S. filifolia*, location of populations, and seed morphology. All individuals grown in the greenhouse produced fruits, suggesting that *S. filifolia* is self-compatible and autogamous (or, possibly, apomictic). Although outcrossing may occur in natural populations, pollinators do not appear to be required for successful seed production (and potential pollinators have not been observed visiting flowers). The capacity for autogamous or apomictic seed production limits gene flow through pollen movement. Potential gene flow through seed movement is also limited in this species. Populations are located near the tops of ridges and the small seeds, lacking any special dispersal mechanism, are likely to tumble or be washed downhill.

It is possible that the alleles found exclusively in West Ridge may also exist in the other two populations, but it is unlikely that they are found in equally high frequencies. Although sample sizes were low owing to the rarity of this species, sampling error is insufficient to explain the observed differences between the populations. Assuming random distribution of alleles, the probability of not detecting an allele actually present at a frequency of 0.25 in a sample of 15 individuals is less than 0.0002; even assuming a completely selfing population (consisting exclusively of homozygotes), the probability of not detecting such an allele is less than 0.02. A more significant issue for a cryptic species in which population differentiation can be maintained over very short distances, such as *S. filifolia*, is that undiscovered populations may harbor additional genetic variation. Genetic variation may be more severely underestimated by lack of sampling of additional populations (or reduced by the extirpation of such populations) than by small sample sizes.

Implications for Conservation

The federally endangered *S. filifolia* is endemic to the Channel Islands, and is currently known from three populations clustered at the southern tip of San Clemente Island, and from scattered individuals nearby and on Santa Catalina Island. Populations range in size from a few to several hundred individuals, and usually vary from one year to another. Thus, this taxon has a narrow range, few populations, and usually small populations. In spite of this rarity, *S. filifolia* on San Clemente Island is not completely devoid of genetic variation; the levels of genetic variation we observed, although low, are not atypical of endemic species. However, because of small and fluctuating population size (which reduces effective population size) genetic drift is likely to continue eroding the remaining genetic diversity in these populations. It will be important to keep populations as large as possible because loss of alleles through genetic drift can cause the random loss of even favorable alleles (Hartl 1988). The loss of alleles is unlikely to be counteracted in this species by the reintroduction of alleles through gene flow. The differentiation of populations separated by only 50 or 100 m thus has a significant conservation implication; drift appears to be a more potent evolutionary force than gene flow in these populations.

The three remaining populations of *S. filifolia* on San Clemente Island are not equivalent genetically. Only West Ridge appears to maintain genetic variation at allozyme loci, suggesting that this population is especially valuable as a source of material for reintroductions or for ex situ collections, which are essential as a safeguard against possible future extirpation in narrow-ranging taxa with few populations (Lande 1988; Simberloff 1988). Loss of this population would cause a significant loss of allozyme variation for *S. filifolia*.

The allozyme data clearly demonstrate low genetic variation and the existence of significant differences among nearby populations. However, conclusions regarding the relative genetic value of different populations may be premature. First, only two polymorphic loci were detected. Other molecular markers more likely to detect polymorphism, such as RAPDs, will permit stronger conclusions regarding the relative value of these populations for reintroductions and ex situ collections. Second, there appears to be only a weak correlation between variation in molecular markers, such as allozymes, and quantitative genetic variation (Reed and Frankham 2001). Molecular markers may offer insights into immediate fitness (through inbreeding depression in small populations leading to reduced population survival, for example; e.g., Newman and Pilson 1997), but long-term survival may also depend on quantitative genetic variation allowing adaptation to changing environments. Surveys of quantitative genetic variation will be important to evaluate the long-term prospects for *S. filifolia*.

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THE CIÉNEGA DE CAMILO: A THREATENED HABITAT IN THE SIERRA MADRE OCCIDENTAL OF EASTERN SONORA, MEXICO

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ABSTRACT

A spring with *Sphagnum palustre* (peatmoss) in the Ciénega de Camilo in eastern Sonora, Mexico, is a new habitat for Sonora and the Sierra Madre Occidental. The vascular plant flora in an area of 0.2 km^2 contains 207 species in 63 families, dominated by Compositae (41 species), Leguminosae (24 species), and Gramineae (21 species). Of these species, 40.1% do not reach Arizona or New Mexico, 15.0% are rare or restricted in Sonora, and only 2.9% are non-native. Pollen analyses of organic mud in a core from the Ciénega recorded pine-oak forest progressively drying in the last 1000 years. The Ciénega de Camilo with its unique peat habitat, diverse flora, and its paleoecological potential is in urgent need of protection.

RESUMEN

Una turbera de *Sphagnum palustre* (musgo) en la Ciénega de Camilo en la parte oriental de Sonora, se considera un habitat nuevo para Sonora y la Sierra Madre Occidental. La flora vascular en un área de 0.2 km^2 contiene 207 especies distribuidas en 63 familias, dominadas por Compositae (41 especies), Leguminosae (24 especies) y Gramineae (21 especies). De estas especies, 40.1% no se presentan en Arizona o New Mexico, 15% son escasas o restringidas a Sonora y solamente el 2.9% son introducidas. Por medio de análisis de polen del barro orgánico obtenido de un núcleo de la ciénega se encontró que el bosque de pino-encino empezó a secarse en forma progresiva los últimos 1000 años. La Ciénega de Camilo con su habitat de turbera único, su diversa flora y su potencial paleoecológico se encuentra en una necesidad urgente de protección.

Key Words: Ciénega de Camilo, Sierra Madre Occidental, Sonora, *Sphagnum palustre*, vascular plants.

As part of a general floristic survey of the Municipio de Yécora in the Sierra Madre Occidental of eastern Sonora (Reina et al. 1999), we encountered a spring with peatmoss mounds at the Ciénega de Camilo. Ciénega is the Spanish term for a marsh or wetland. Considering the uniqueness of this habitat for Sonora and Mexico, we discuss the vegetation, flora, and conservation concerns.

Geographic Setting

Location. The Ciénega de Camilo is at 1550 m elevation 8.0 km west of the Mountain Pima village of El Kípor (12.6 km east of Maycoba, 8.5 km west of the Chihuahua border) on Mexico Highway 16 (MEX 16; 28°25′34″N, 108°34′09″W; Fig. 1). The stream at Camilo flows easterly, turns north and soon joins the westerly-flowing Río Yepáchic. Downstream the Río Yepáchic meets the Río Yécora to flow north as the Río Mulatos, a major tributary of the Río Yaqui. Although most of the Mesa del Campanero-Yécora-Camilo area is in the southeastern portion of the Río Yaqui drainage basin, the area is within the broad Río Mayo Region of Gentry (1942) and Martin et al. (1998). The drainage

of the Río Mayo proper begins immediately to the south. The area from Yepáchic, Chihuahua, west to Yécora is the core area for the Mountain Pima Indians. With the completion of MEX 16 in 1992, traveling between Hermosillo or Ciudad Obregón, Sonora, and Ciudad Chihuahua became relatively easy for the first time. The new highway opened the Sierra Madre Occidental to many new economic and cultural activities.

METHODS

The Ciénega de Camilo was visited 15 times from 1996 to 2000 in the following months: March (5), April (2), May (1), June (1), July (1), and September (6). Notes were made on the vegetation and flora. A total of 146 plant collections (250 specimens including duplicates) were made in an area of 0.2 km^2 from the north-northwest slope above the highway across the canyon to above the Ciénega on the south-southeast slope. The specimens were deposited in herbaria at the University of Arizona, University of Texas, Universidad Autónoma de México, Rancho Santa Ana Botanic Garden, Universidad de Sonora, and 16 other institutions. Collaborating systematists identified many specimens. The flora is summarized in Appendix 1. Local common names were obtained through interviews with Mountain Pima Indian and mestizo res-
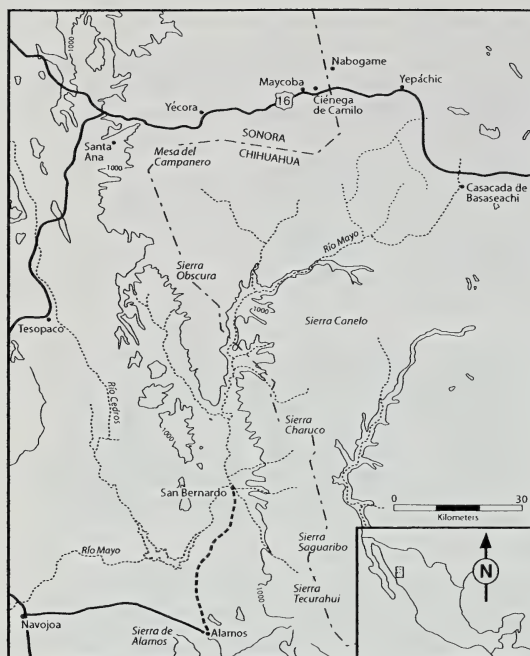
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idents. Pollen samples were deposited into the reference collection in the Instituto Ecología-UNAM in Hermosillo. Voucher specimens of common, distinctive species not collected in the study area were collected elsewhere in the Municipio de Yécora (Reina et al. 1999).

Water samples were collected on March 15, 2000 from the springhead and from the arroyo about 200 m upstream of the Ciénega outflow for later analyses in the Soil, Water, and Plant Analysis Laboratory at the University of Arizona. Four cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) and six metals (Cu^{2+}, Fe^{3+}, Hg^+, Mo^+, Pb^{2+}, and Zn^{2+}) were analyzed using an inductively coupled argon plasma emission spectrophotometer. Six anions (Br^-, Cl^-, F^-, NO_3^-, PO_4^{3-}, and SO_4^{2-}) were analyzed using an ion chromatograph.

RESULTS AND DISCUSSION

Climate. The climate of the Sierra Madre Occidental in eastern Sonora is dramatically cooler than that of the Sonoran Desert lowlands to the west (Búrquez M. et al. 1992). The mean annual temperature at Yécora is 14.4°C with extended periods of freezing temperatures. Rainfall is biseasonal with most occurring in summer (June–October) and less in winter (November–February). The mean annual precipitation at Yécora is 913 mm/yr (Hastings and Humphrey 1969; INEGI 1988; Búrquez M. et al. 1992). Rainfall appears to increase with elevation from Yécora at 1500 m elevation to over 2200 m

on Mesa del Campanero. We estimate the rainfall at the Ciénega de Camilo to be more than 1000 mm/yr.

Lowe (1964) summarized the rainfall for biotic communities in Arizona and New Mexico: desert-scrub (254 mm/yr), desert grassland (279 mm/yr), pinyon-juniper woodland (432 mm/yr), and *Pinus ponderosa* (ponderosa pine, 533 mm/yr), *Pseudotsuga menziesii* (Douglas fir, 660 mm/yr), and *Picea* spp.-*Abies lasiocarpa* (spruce-alpine fir, 864 mm/yr) forests. The rainfall for Yécora is greater than the rainfall anywhere in Arizona where only a few high peaks average more than 760 mm/yr and only in occasional years receive more than 900 mm (Sellers and Hill 1974). Thus, the grasslands, oak woodlands, and pine-oak forests of eastern Sonora receive much more precipitation, and less of it as snow, than their Arizona counterparts.

Vegetation. The Ciénega is in the bottom of a deep, rocky stream canyon in dense pine-oak forest. Common trees are *Pinus engelmannii* and *P. yecorensis* and eight species of *Quercus*, while *P. chihuahuana*, *P. herrerae*, *Juniperus deppeana*, and *Arbutus xalapensis* are present. The shaded understory supports *Pseuderanthemum praecox*, which has showy purple flowers on leafless stems in March. Mossy boulders are covered with *Polypodium polypodioides*, *Selaginella rupincola*, *S. novoleonensis*, and *Echinocereus scheeri*. Riparian trees include *Alnus oblongifolia*, *Cupressus arizonica*, *Ilex tolucana*, *Juniperus mucronata* (closely related to *J. scopulorum*; Adams 2000), and *Prunus gentryi*. On the south slope around the Ciénega, the forest is more open with oaks, especially *Quercus chihuahuensis*, more important.

The Ciénega is in an opening in the forest on the south-southeast-facing side of the canyon. Permanent water emerges from a springhead and flows through the Ciénega into the stream below. In the Ciénega, *Sphagnum palustre* (peatmoss) forms hummocks of dark mud. Occasional ferns (*Athyrium filix-femina*, *Plagiogyria pectinata*), grasses (*Agrostis scabra*, *Andropogon glomeratus*, *Panicum acuminatum*), sedges (*Carex turbinata*, *Cyperus* spp., *Eleocharis* spp., *Juncus* spp., *Rhynchospora* sp.), and *Rubus* sp. (raspberry) are scattered in the Ciénega. In September, the abundant scarlet flowers of *Lobelia cardinalis* (cardinal flower) were visited by resident *Hylocharis leucotis* (white-eared hummingbird) and migrant *Selasphorus rufus* (rufous hummingbird). A few trees (*Arbutus xalapensis*, *Ilex tolucana*, and *Quercus coccolobifolia*) are on a mound within the Ciénega.

On the east side of the Ciénega, there is an open grassy meadow on whitish soils, indicating that the spring was much larger in the past. Important plants include grasses (*Bouteloua hirsuta*, *Lycurus phalaroides*), legumes (*Dalea albiflora*, *D. filiformis*, *Desmodium* spp., *Eriosema palmeri*, *Macroptilium gibbosifolium*), *Eryngium lemmonii*, and diverse

herbs. The subshrub *Mimosa pauli* is locally common.

Flora. Sphagnum. The genus *Sphagnum* with something less than 200 species occurs in many parts of the world, especially in temperate and boreal latitudes (Crum 1984). Seven species have been reported for Mexico, mostly in the southeastern states of Hidalgo, Oaxaca, and Veracruz. Interestingly, all of these species are southern disjunct populations of temperate species that are widespread at high latitudes in North America and Eurasia, and not tropical species. The only *Sphagnum* record from northern Mexico was a 1937 collection by Harde LeSueur of *S. squarrosum* Crome from near Chuichupa, Municipio de Madera, Chihuahua (Crum 1980; ca. 145 km north-northeast of Camilo). The peatmoss at Camilo was identified by Lewis E. Anderson as *S. palustre,* the type species for the genus *Sphagnum* described by Linnaeus in 1753 from a European collection. This species occurs in many kinds of mineral-rich swampy habitats (Crum 1984). The only previous Mexican localities for this species were from Hidalgo and Veracruz (Crum 1984).

On March 15, 2000, water temperatures were 19.4°C as it emerged from the ground, 20.0°C in the peatmoss in shade, and 22.2°C in the open at the edge of the peatmoss. Water in the shady arroyo was 11.1°C. The water was acidic (pH = 4.2 at emergence and 4.5 in the arroyo), very likely due to small amounts of hydrothermally mineralized water moving from deep in the earth upward through cracks in the middle Tertiary andesites (Robert Scarborough personal communication). Analyses of a suite of 16 minerals, salts and metals showed that the Ciénega water was essentially pure with only modestly elevated sulfate (44.5 ppm) content. In contrast the arroyo water had higher levels of calcium (82.8 ppm), magnesium (14.0 ppm), sodium (20.2 ppm), nitrates (1.4 ppm), sulfates (158.2 ppm), molybdenum (77 ppb), and zinc (92.5 ppb).

Analyses of the pollen in the organic mud trapped under the peatmoss on the hummock demonstrated that the Ciénega de Camilo has supported a pine-oak forest for at least the last 1000 years (radiocarbon date of 980 ± 70 yr B.P. [radiocarbon years before 1950; Beta 144443] at 40–60 cm depth; Ortega R. 2000; Ortega R. et al. in press). Declines in fern spores suggest that the vegetation became progressively more xeric toward the present.

Flora. Vascular plants. The total number of vascular plants was 207 species in 152 genera and 63 families. Some of the records were included in Martin et al. (1998) and Van Devender et al. (in press). The families with the most species were Compositae (41), Leguminosae (24), and Gramineae (21). Only six species (2.9%) were non-native: *Cynodon dactylon, Eleusine indica, Prunella vul-*

garis, Rumex crispus, Setaria pumila, and *Taraxacum officinale.* Comparison with Lehr (1978), Bowers and McLaughlin (1996), and Roalson and Allred (no date) indicate that 83 species (40.1%) in the Camilo flora are primarily Mexican species not found in Arizona or New Mexico, although seven of them have been reported for Texas (Correll and Johnston 1970; Appendix 1). However, 66 (31.9%) and 69 (33.3%) Camilo species were not shared with the floras of Nabogame (600 species, 40 km², 1600–2100 m elevation, Laferrière 1994; 19 km to the east) or the Parque Nacional Cascada de Basaseachi (823 species, 65 km², 850–2100 m elevation, Spellenberg et al. 1996; ca. 50 km to the southeast) in Chihuahua.

About 30 species (14.5%) in the Camilo local flora may be considered rare or have restricted distributions in Sonora. Howard Gentry's 1942 Río Mayo Plants and its revision (Martin et al. 1998) with a total of 2825 taxa are the primary references in assessing rarity. This is a broad area that includes all of southeastern Sonora from the Río Yaqui south to the Sinaloa border, and the Cascada de Basaseachi (Spellenberg 1996) and Nabogame (Laferrière 1994) in western Chihuahua. Seven Camilo species are not reported in Martin et al. (1998): *Cyperus sphaerolepis, Eleocharis minima* (Cyperaceae; Roalson 2002), *Desmodium grahamii* (Leguminosae), *Juncus dichotomus* (Juncaceae), *Laennecia filaginoides* (Compositae), *Ludwigia palustris* (Onagraceae), and *Plagiogyria pectinata* (Plagiogyraceae). Another ten species were reported from the Chihuahuan portion of the Río Mayo region but not for Sonora: *Athyrium filix-femina* (Dryopteridaceae), *Cirsium* sp. nov, *Erigeron fundus, Hieracium abcissum, Simsia amplexicaulis* (Compositae), *Desmodium neomexicanum* (Leguminosae), *Juncus effusus* (Juncaceae), *Salvia hispanica* (Labiatae), and *Schizachyrium sanguineum* var. *hirtiflorum* (Gramineae). The Camilo collection of *Senecio riomayensis* was reported in Martin et al. (1998). This delicate spring annual was previously only known from the type locality on Mesa de Abajo, Chihuahua (Turner 1993). *Cirsium* sp. and *Euphorbia* sp. are undescribed species from eastern Sonora and western Chihuahua (Guy L. Nesom and Victor W. Steinmann personal communications). At least ten Camilo species are mostly or completely endemic to the Río Mayo Region (Appendix 1).

Thirteen other species in the Camilo flora were previously reported from the Sonoran portion of the Río Mayo Region but from few localities. Eight species were known from a single locality: *Carex turbinata, Cyperus niger, Scleria reticularis* (Cyperaceae), *Cyclanthera minima* (Cucurbitaceae), *Lechea tripetala* (Cistceae), *Mimulus calciphilus* (Scrophulariaceae), *Opuntia* cf. *durangensis* (but see Paredes et al. 2000), *Oxalis hernandesii* (Oxalidaceae), and *Panicum acuminatum* (Gramineae). Four species were reported from two localities: *Arenaria lanuginosa* subsp. *saxosa* (Caryophylla-

ceae), *Desmodium molliculum* (Leguminosae), *Gongylocarpus rubricaulis,* and *Passiflora quercetorum* (Passifloraceae), and *Senecio sandersii* (Compositae). The other Sonoran localities for these 12 species are in the series of ranges on the west front of the Sierra Madre Occidental roughly oriented north-south along the Sonora-Chihuahua border: Mesa del Campanero, the sierras Obscura, Charuco, Saguaribo, and Tecurahui, and the Sierra de Alamos isolated to the southwest (Fig. 1; Martin et al. 1998).

Conservation. The spring at the Ciénega de Camilo with acidic warm water and well developed peat mounds is a unique habitat for Sonora, and probably for the Sierra Madre Occidental and northern Mexico in general. The habitat for Le-Sueur's collection of *Sphagnum squarrosum* from Chihuahua was not reported and may have been degraded in the last 60 years.

With 207 species, the flora of such a small area (0.2 km^2) is very diverse with only 2.9% non-native species. As discussed above seven species were added to the flora of the overall Río Mayo Region, and nine to the Sonoran part of it. About 15% of the flora is considered rare or of limited distribution in Sonora. Nineteen species (9.2%) of Camilo plants that are of special concern for Sonora are being tracked in the database of the Centro de Datos para la Conservación at the Instituto del Medio Ambiente y Desarrollo Sustentable del Estado de Sonora (IMADES). The fern *Plagiogyria pectinata* at Camilo is the only Sonoran record for the family Plagiogyraceae.

Exposed dark organic mud around the active wetland indicates that the Ciénega has been shrinking in recent years. Livestock use and other ranching related activities are the impacts on the habitat. In wet years when the Ciénega is saturated, cattle can only enter the edges without becoming mired. However, winter-spring drought conditions for three years between 1997 and 2001 reduced the water content of the Ciénega for part of the year. The numbers of rushes, flat sedges, and grasses, especially *Andropogon glomeratus,* in the *Sphagnum* areas have increased dramatically. The lower portion of the Ciénega above the arroyo is now seriously disturbed by hooves, and the edges of the lower peat mounds are beginning to erode. The owner has trenched a small channel through the peatmoss and dug out a small pool for the cattle to drink.

If this unique habitat is to survive, it is in urgent need of protection. Fortunately, the protection measures are simple and relatively inexpensive. The cattle should be kept away from the Ciénega and the water allowed to flow naturally through the vegetation. The water would still be available for livestock use in the arroyo below. The study of the flora of this rare ciénega, the demonstration of the uniqueness of the association, and this report

should be, we urge, the first step in the protection of the Ciénega de Camilo.

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APPENDIX 1

PLANTS AT THE CIÉNEGA DE CAMILO, MUNICIPIO DE YÉCORA, SONORA

Collector's numbers in parentheses: ALRG = Ana L. Reina G., CIO = Carmen I. Ortega R., TRV = Thomas R. Van Devender. Specimens without voucher numbers are observations. Symbols: * = immediate vicinity of ciénega, + = introduced species, ◆ = not in Arizona or New Mexico, ◆◆ = occurs in Texas but not Arizona or New Mexico, ◀ = Río Mayo endemic. Common name order: Spanish, Mountain Pima, English.

Moss

Sphagnaceae

*Sphagnum palustre L. Musgo pantanoso; peatmoss. [TRV 97-836].

Ferns and Fern Allies

Aspleniaceae

Asplenium palmeri Maxon. Siemprevive; spleenwort. [TRV 97-850]

Dryopteridaceae

*Athyrium filix-femina (L.) Roth ex Mertens. Lady fern. [TRV 97-835]

Plagiogyraceae

* ◆ Plagiogyria pectinata (Liebm.) Lell. [TRV 97-831]

Polypodiaceae

◆ ◆ Polypodium polypodioides (L.) Watt. var. aciculare Weatherby. Oijik hehevil (Pima).

Pteridaceae

Bommeria hispida (Mett. ex Kuhn) L. Underw. [TRV 97-851, 98-346]
Cheilanthes bonariensis (Willd.) Proctor. Hierba negra, hierba del zorrillo; oijik hehevil, tu tok totum (Pima).
◆ ◆ Cheilanthes kaulfussii Kunze [TRV 98-346A]

Selaginellaceae

Selaginella novoleonensis Hieron. Flor de la piedra; resurrection plant.
Selaginella rupincola L. Underw. Siemprevive; spike moss. [TRV 96-104]

Gymnosperms

Cupressaceae

*Cupressus arizonica E. Greene. Sabino; shorlak ga'a (Pima); Arizona cypress.
*Juniperus deppeana Steud. Táscate, ga'a (Pima); alligator bark juniper. [CIO sn.]
* ◆ ◀ Juniperus mucronata R.P. Adams. Táscate finito, táscate colorado, sabino; uu ga'a (Pima); Maycoba juniper.

Pinaceae

*Pinus chihuahuana Engelm. Pino chino; bijik muk juk, huk juk (Pima); Chihuahua pine. [ALRG 96-278, CIO sn.]
*Pinus engelmannii Carr. Pino blanco; Apache pine.
* ◆ Pinus herrerae Mart. Pino chino.
* ◆ ◀ Pinus yecorensis Debreczy & Racz. Pino colorado; Yécora pine. [ALRG 96-279]

Dicots

Acanthaceae

Elytraria imbricata (Vahl) Pers. Cordoncillo.
♦ *Pseuderanthemum praecox* (Bentham) Leonard [TRV 97-402, 98-1832]

Amaranthaceae

Gomphrena decumbens Jacq. Globe amaranth. [ALRG 2000-649]

Anacardiaceae

*Rhus aromatica Ait. Limita, lima, hierba del venado; cotatemech (Pima); skunk bush. [TRV 98-348]
*Rhus radicans L. Hiedra; poison ivy.

Apocynaceae

♦ *Mandevilla foliosa* (Muell. Arg.) Hemsl. Hierba del piojo. [TRV 97-824]

Aquifoliaceae

* ♦ *Ilex tolucana* Hemsl. [CIO sn., TRV 97-838]

Asclepiadaceae

* ♦ *Asclepias ovata* Mart. & Gal. Milkweed. [TRV 97-834]

Begoniaceae

♦ *Begonia gracilis* H.B.K. Cañaigra, geranio; shu'pal (Pima); begonia.

Betulaceae

*Alnus oblongifolia Torrey. Alamillo; cúmpu (Pima); Arizona alder. [TRV 96-99]

Cactaceae

♦ *Echinocereus scheeri* (Salm-Dyck) Scheer. Choyita, choya; hedgehog cactus.
♦ *Mammillaria standleyi* (Britton & Rose) Orcutt. Pitahayita; pincushion cactus.
♦ *Opuntia* aff. *durangensis* Britton & Rose. Nopal; na'ub (Pima); Durango prickly pear.

Campanulaceae

*Lobelia cardinalis L. subsp. *graminea* (Lam.) McVaugh. Cardinal flower. [ALRG 97-1416, TRV 98-1844]

Caryophyllaceae

*Arenaria lanuginosa (Michx.) Rohrb. subsp. *saxosa* (A. Gray) Maguire. Sandwort. [ALRG 2000-657, TRV 98-1834]
Cerastium texanum Britton. Mouse-ear chickweed. [TRV 97-409]

Cistaceae

* ♦ *Lechea tripetala* (Moc. & Sessé) Britton [ALRG 97-1415]

Compositae

* ♦ *Acourtia dieringeri* R.L. Cabrera. Espantamula; Pipichagua (Pima); brownfoot.

♦ *Astranthium orthopodum* (H. Rob. & Fern.) Larsen [TRV 98-1841]
Baccharis salicifolia (Ruiz & Pavon) Pers. Batamote; bachom, vashen (Pima); seep willow.
*Bidens aurea (Ait.) Sherff [TRV 98-1839]
*Bidens heterosperma A. Gray [TRV 2001-820B]
*Bidens lemmoni A. Gray. var. *lemmonii*. Saitilla, aceitilla; beggar ticks. [ALRG 98-1823, TRV 98-1819]
*Bidens pilosa L. Saitilla, aceitilla; beggar ticks. [TRV 98-1823]
Brickellia betonicifolia A. Gray [TRV 98-1833]
*Brickellia simplex A. Gray [TRV 98-1843]
♦ ◄ *Cirsium* sp. nov. Cardo; thistle. [ALRG 97-1407, 2000-213]
Conyza canadensis (L.) Cronq. Cola de zorra; jarilla; horseweed.
*Cosmos parviflorus (Jacq.) Pers.
♦ *Erigeron fundus* Nesom. Fleabane. [TRV 97-410]
* ♦ *Gamochaeta americana* (Mill.) Wedd. Cudweed. [TRV 97-837, 99-586]
Heterosperma pinnatum Cav.
Heterotheca subaxillaris (Lam.) Britton & Rose. Árnica; camphor weed.
♦ *Hieracium abscissum* Less. Hawkweed. [TRV 97-826, 97-847]
*Hieracium pringlei A. Gray. Hawkweed. [ALRG 97-1406]
* ♦ *Jaegeria hirta* Less.
♦ ♦ *Laennecia filaginoides* DC. [TRV 98-1836]
*Lasianthaea podocephala (A. Gray) K. Becker. Pionía; marmatham (Pima).
♦ *Melampodium* cf. *appendiculatum* B.L. Rob. Rosamaría.
♦ *Melampodium cupulatum* A. Gray
* ♦ *Milleria quinqueflora* L. Hoja ancha.
Pectis prostrata Cav.
* ♦ *Perityle microcephala* A. Gray. Rock daisy. [ALRG 97-1409, TRV 98-1848, 98-1849]
Pseudognaphalium arizonicum (A. Gray) Anderb. Arizona cudweed. [TRV 99-585]
* ♦ *Pseudognaphalium stramineum* (H.B.K.) Anderb. Cudweed. [TRV 97-843]
♦ *Ratibida mexicana* (S. Watson) J.M. Sharp. San Pedro; hogana (Pima); Mexican coneflower. [TRV 99-584]
*Senecio carlomasonii B.L. Turner & T.M. Barkley. Hoja ancha, pintapán; comrajaka (Pima); Madrean groundsel.
♦ ◄ *Senecio riomayensis* B.L. Turner. Mayo groundsel. [TRV 96-102]
Senecio salignus DC. Ruina.
♦ ◄ *Senecio sandersii* B.L. Turner. Sanders groundsel. [TRV 99-628]
♦ *Simsia amplexicaulis* (Cav.) Pers. Rosamaría.
Stevia plummerae A. Gray var. *plummerae* [TRV 99-589]
* ♦ *Tagetes filifolia* Lag. Anisillo; licorice marigold.
* ♦ *Tagetes subulata* Cerv. ex La Llave. Marigold. [TRV 98-1828]
* ♦ *Tagetes triradiata* Greenm. Cempoalillo; marigold. [TRV 98-1831]
+ *Taraxacum officinale* Weber. Diente de león; dandelion.
*Zinnia peruviana (L.) L. India; wild zinnia.
* ♦ *Zinnia zinnioides* (H.B.K.) Olorodes & Torres. India.

Convolvulaceae

Ipomoea cristulata Hallier f. Trompillo; scarlet morning glory.
Ipomoea cf. *purpurea* (L.) Roth. Trompillo, flor azul; tu'tu'gioschski (Pima); morning glory.

Crassulaceae

♦ *Sedum* cf. *mellitulum* Rose. Stonecrop. [TRV 98-347]

Cruciferae

Descurainia pinnata (Walt.) Britton. Pamita; tansy mustard.

Dryopetalon runcinatum A. Gray var. *laxiflorum* Rollins. [TRV 96-101, 97-408]

Cucurbitaceae

♦ *Cucurbita argyrosperma* Huber subsp. *argyrosperma* var. *palmeri* (L.H. Bailey) Merrick & Bates. Calabaza; coyote melon. [TRV 98-1817]

♦ ◄*Cyclanthera minima* (S. Watson) Kearns & C.E. Jones

Ericaceae

*Arbutus xalapensis H.B.K. Madroño colorado; madrone. [TRV 97-401]

Arctostaphylos pungens H.B.K. Manzanilla, manzanilla del monte; ioly, jagar yoel (Pima); manzanita.

Euphorbiaceae

♦ *Euphorbia anychioides* Boiss. [ALRG 97-1405]

*♦ Euphorbia subreniformis S. Watson. [TRV 98-1830]

*♦ ◄Euphorbia sp. nov. [TRV 96-103, 97-404, 98-349]

*Tragia nepetifolia Cav. var. *dissecta* Muell. Arg. Ortiguilla; bi ipil (Pima); noseburn. [ALRG 97-1413, TRV 97-825]

Fagaceae

*Quercus arizonica Sarg. Encino blanco; shiparr, toá toá (Pima); Arizona oak.

*♦Quercus chihuahuensis Trel. Encino peludo; toá toá ush (Pima); Chihuahua oak. [CIO sn.]

*♦Quercus coccolobifolia Trel. Güeja, cusi; hopakily, toá ush (Pima). [CIO sn.]

*♦Quercus durifolia Seem. Cusi barril; shiparr, shiprus. vashily (Pima). [CIO sn.]

*Quercus hypoleucoides A. Camus. Cusi prieto, shiparr (Pima); silverleaf oak. [CIO sn.]

*Quercus oblongifolia Torrey. Encino, encino azul; Mexican blue oak. [TRV 97-848]

Quercus toumeyi Sarg. Encino finito, encino gallinero; viikam toá (Pima); Toumey oak.

Geraniaceae

♦ *Geranium deltoideum* Rydb. Quelite pata de cuervo; geranium.

Hypericaceae

♦ *Hypericum moranense* Kunth.

Labiatae

Agastache mearnsii Wooton & Standley

Monarda citriodora Cerv. subsp. *austromontana* (Epl.) Scora. Orégano de burro, orégano grande; g'burr toncama (Pima); bee balm.

+*Prunella vulgaris* L. Hiosh, jiosh (Pima); self heal.

♦ *Salvia alamosana* Rose. Alamos sage. [TRV 98-1837]

*♦ ♦ Salvia hispanica L. Chia; Spanish sage. [TRV 98-1840]

Salvia tiliaefolia Vahl. Chía.

Leguminosae

♦ ◄*Astragalus gentryi* Standl. Locoweed. [TRV 97-403]

*Calliandra humilis Bentham var. *humilis*

*Chamaecrista nictitans (L.) Moench subsp. *nictitans* var. *mensalis* (Greenm.) Irwin & Barneby. Mautillo, dáis.

Cologania lemmoni A. Gray. Perrito del monte. [TRV 97-840]

*Crotalaria pumila Ortega. Huevitos del toro; bav shavily (Pima); rattlebox.

*Crotalaria sagittalis L. Huevitos del toro; rattlebox.

Dalea albiflora A. Gray. [ALRG 2000-648, TRV 99-593]

Dalea filiformis A. Gray. [TRV 98-1818]

Dalea versicolor Zucc. var. *sessilis* (A. Gray) Barneby. [TRV 97-414, 98-344]

Desmodium angustifolium (H.B.K.) DC. Hierbita del amor; tick clover. [ALRG 2000-654]

Desmodium grahamii A. Gray. Tick clover. [TRV 98-1847]

♦ *Desmodium molliculum* (H.B.K.) DC. Tick clover. [TRV 98-1814]

Desmodium neomexicanum A. Gray. Hierbita del amor; tick clover. [ALRG 2000-655]

* ♦ Eriosema palmeri S. Watson. [ALRG 2000-651]

*Lotus alamosanus (Rose) Gentry [TRV 98-353]

Lotus greenei (Wooton & Standley) Ottley ex Kearney & Peebles [ALRG 2000-150]

Macroptilium gibbosifolium (Ortega) A. Delgado

Mimosa aculeaticarpa Ortega var. *biuncifera* (Bentham) Barneby. Gatuño; wait-a-minute bush. [TRV 98-1851]

♦ ◄*Mimosa pauli* Barneby. Gatuño; joid-jupper (Pima); wait-a-minute bush. [ALRG 2000-656, TRV 98-1842]

Phaseolus acutifolius A. Gray var. *tenuifolius* A. Gray. Frijol; wild bean. [ALRG 2000-652]

Phaseolus parvulus E. Greene. Frijol; wild bean. [TRV 99-591]

♦ *Phaseolus pauciflorus* Sesse & Moc. Frijol; wild bean.

♦ *Vicia pulchella* H.B.K. subsp. *pulchella*. Vetch. [TRV 98-1815]

*Zornia reticulata J.E. Smith. Hierba de la víbora.

Linaceae

♦ *Linum pringlei* S. Watson. White flax. [TRV 98-1816]

Lythraceae

*Cuphea wrightii A. Gray

Malvaceae

Sida neomexicana A. Gray

Onagraceae

♦ *Gongylocarpus rubricaulis* Cham. & Schltdl.

*Ludwigia palustris (L.) Ell. Marsh purslane. [TRV 97-842, 99-234]

Orobanchaceae

Conopholis alpina Liebm. var. *mexicana* (A. Gray) Hayne. [TRV 97-412]

Oxalidaceae

Oxalis corniculata L. Saladita; wood sorrel.

♦ *Oxalis hernandesii* DC. Saladita; wood sorrel.

Passifloraceae

♦ ◄*Passiflora quercetorum* Killip. Talayote; passionflower.

Phytolaccaceae

Phytolacca icosandra L. Masorquilla; pokeberry. [TRV 97-841]

Polygalaceae

Monnina wrightii A. Gray
**Polygala glochidiata* H.B.K. Purple milkwort.

Polygonaceae

**Polygonum* sp.
*+*Rumex crispus* L. Cañaigra, chile de agua; curly dock.
**Rumex* cf. *obtusifolius* L. Cañaigra, chile de agua; dock.

Ranunculaceae

Ranunculus arizonicus Lemmon. Arizona buttercup. [TRV 97-413]
Thalictrum cf. *fendleri.* Meadow rue.

Rhamnaceae

* ♦ *Ceanothus buxifolius* Willd. Junqui (Pima); buckbrush. [T.F. Daniel 8618]
**Rhamnus* sp. Ojo de venado; shiik wupil (Pima); coffeeberry.

Rosaceae

* ♦ *Prunus gentryi* Standl. Capulín arroyero; aguasique, mo'oshkam (Pima); Gentry cherry. [TRV 96-100 (discarded)]
Prunus serotina Ehrh. subsp. *virens* (Wooton & Standley) McVaugh. Capulín, cheri; aguasique, jumpil, humpil (Pima); wild cherry. [TRV 98-352]
**Rubus* sp. Rosalía, alejandría, zarzamora; raspberry. [TRV 97-846, 99-232]

Rubiaceae

* ♦ *Crusea longifolia* (Willd. ex. Roemer & Schultes) W.R. Anderson. [TRV 99-582)
♦ *Crusea psyllioides* (Kunth) W.R. Anderson. [TRV 98-1838]
**Crusea wrightii* A. Gray var. *wrightii.* [TRV 99-588]
**Galium* sp. Bedstraw.
**Mitracarpus hirtus* (L.) DC.

Saxifragaceae

Heuchera sanguinea Engelm. Cañaigra; coral bells. [TRV 98-345]

Scrophulariaceae

♦ *Mimulus calciphilus* Gentry. Monkey flower. [TRV 97-411]

Solanaceae

Solanum nigrescens Mart. & Gal. Chiquequelite, chichequelite; nightshade. [TRV 99-592]

Umbelliferae

**Eryngium lemmonii* J.M. Coult. & Rose. Hierba del sapo; button snakeroot. [TRV 98-1845]

Valerianaceae

Valeriana sorbifolia Kunth var. *sorbifolia.* Valerian.

Verbenaceae

Glandularia bipinnatifida (Nutt.) Nutt. var. *latifolia* Perry. Verbena. [TRV 98-343]
♦ *Priva mexicana* (l.) Pers. [ALRG 2000-647]
**Verbena carolina* L. Verbena.
**Verbena neomexicana* (A. Gray) Small. Verbena.

Violaceae

♦ *Viola percrenulata* H. Ballard, ined. Violet. [TRV 97-405]

Vitaceae

Vitis arizonica Engelm. Uva del monte; wild grape.

Monocots

Agavaceae

♦ *Agave polianthiflora* Gentry. Amolillo; redflower striped agave.

Bromeliaceae

* ♦ *Tillandsia erubescens* Schltdl. Flor de encino; cu'uchui (Pima). [TRV 98-351]
Tillandsia recurvata L. Ball moss.

Commelinaceae

**Commelina dianthifolia* Delile. Dayflower.
Tradescantia pinetorum E. Greene. Spiderwort.
* ♦ *Tripogandra purpurascens* (Schauer) Handlös

Cyperaceae

* ♦ *Carex turbinata* Liebm. Sedge. [TRV 98-350]
**Cyperus niger* Ruiz & Pavon. Flat sedge. [TRV 98-1821, 98-1822]
**Cyperus sphaerolepis* Boeck. Flat sedge. [ALRG 97-1412]
* ♦ ♦ *Eleocharis minima* Kunth. [TRV 98-1827]
**Eleocharis montevidensis* Kunth. Spike rush. [TRV 87-845]
Fimbristylis dichotoma (L.) Vahl. [ALRG 2000-658]
* ♦ ♦ *Rhynchospora* sp. [TRV 97-849]
* ♦ *Scleria reticularis* Michx. [TRV 98-1846]

Gramineae

**Agrostis scabra* Willd. Bentgrass. [TRV 97-832, 98-354]
**Andropogon glomeratus* (Walt.) B.S.P. Bushy beardgrass. [ALRG 97-1408]
**Bouteloua hirsuta* Lag. Hairy grama.
Bromus anomalus Rupr. ex E. Fourn. Nodding brome.
Chloris virgata Swartz. Feather fingergrass.
*+*Cynodon dactylon* (L.) Pers. Bermuda grass.
**Digitaria ciliaris* (Retz.) Koeler. Crabgrass. [ALRG 97-1411, TRV 98-1835]
*+*Eleusine indica* (L.) Gaertn. Goose grass.
Eragrostis intermedia Hitchc. Plains lovegrass.
**Hackelochloa granularis* (L.) Kuntze. [TRV 99-588]
♦ *Lycurus phalaroides* H.B.K. Wolftail. [TRV 98-1829]
♦ *Muhlenbergia alamosae* Vasey. Alamos muhly. [TRV 97-406]
**Muhlenbergia* sp. Annual muhly.
* ♦ *Oplismenus burmannii* (Retz.) P. Beauv. Zacate salado.
* ♦ *Panicum acuminatum* Swartz. [TRV 97-828]
**Panicum bulbosum* H.B.K. Bulb panicgrass.
* ♦ ♦ *Paspalum convexum* Humb. & Bonpl. [ALRG 2000-653, TRV 98-1820]

◆ *Pereilema crinitum* Presl [TRV 97-407]
◆ *Schizachyrium brevifolium* (Swartz) Nees ex Buse
  [TRV 98-1829A]
Schizachyrium sanguineum (Retz) Alston var. *hirtiflorum*
  (Nees) Hitchc. [TRV 99-590]
+*Setaria pumila* (Poir.) Roemer & Schultes. Bristlegrass.

Iridaceae

Nemastylis tenuis (Herb.) S. Watson. Violeta.

Juncaceae

*Juncus acuminatus Michx. Rush. [TRV 97-829, 97-852,
  98-1825, 98-1826]

*Juncus dichotomus Ell. Rush. [TRV 98-1850]
*Juncus effusus L. Rush. [TRV 97-844]
*Juncus marginatus Rostk. Rush. [TRV 97-833, 98-1824]

Liliaceae

◆ *Echeandia palmeri* Cruden. Palmer crag lily.

Orchidaceae

◆ *Corralorhiza odontorhiza* (Willd.) var. *pringlei*
  (Greenm.) Freudenstein. Coral root. [ALRG 97-1415A]
◆ *Malaxis fastigiata* (Reichb. f.) Kuntze. Quiqui. [TRV
  97-839]

NAVARRETIA WILLAMETTENSIS AND NAVARRETIA SAXIMONTANA (POLEMONIACEAE), NEW SPECIES FROM EPHEMERAL WETLANDS OF WESTERN NORTH AMERICA

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Abstract

Navarretia willamettensis is a newly described species inhabiting vernal pools and similar habitats in the Willamette Valley of western Oregon. *Navarretia saximontana* is a newly described species inhabiting ephemeral wetlands of the Rocky Mountains, Colorado Plateau and Great Plains. Both species pertain to the *N. leucocephala* group of *N.* section *Navarretia* and have been confused with *N. intertexta* and *N. leucocephala* subsp. *minima*.

Key Words: Navarretia, vernal pools, willamettensis, saximontana, new species.

Regional floristic treatments of *Navarretia* (e.g., Cronquist 1984, 1959; Wilken 1986) have made note of frequent difficulty in distinguishing between *N. leucocephala* Benth subsp. *minima* (Nutt.) A. G. Day and *N. intertexta* (Benth.) Hook. (*sensu* Day 1993, including subspecies *intertexta* and *propinqua* [Suksd.] A. G. Day). This difficulty has been due, in part, to the existence of two undescribed species: *N. willamettensis,* sp. nov., and *N. saximontana,* sp. nov. *Navarretia willamettensis* is restricted to the Willamette Valley of western Oregon. *Navarretia saximontana* occurs in the United States and southern Canada from the Rocky Mountains and Colorado Plateau eastward into the Great Plains. The existence of these two species first became evident to the senior author during a morphological study of the navarretias of Oregon, and was corroborated by phylogenetic analyses of the genus using morphology and DNA sequence data (Spencer 1997; Spencer and Porter 1997; In those works, *N. willamettensis* is referred to as "Jackson-Frazier", and *N. saximontana* is referred to as "Dog Valley".).

Phylogenetic analyses of nuclear ribosomal DNA (Spencer and Porter 1997) place *N. willamettensis* and *N. saximontana* in *N.* sect. *Navarretia* within the *N. leucocephala* group (*sensu* Day 1993), which includes *N. fossalis* Moran (of southern California and northern Mexico), *N. leucocephala* (of western North America), *N. involucrata* Ruiz & Pav. (of Chile and Argentina), *N. prostrata* (A. Gray) Greene (of central and southern California), and *N. myersii* P. S. Allen & A. G. Day (of northern and central California). Those analyses suggest that *N. saximontana* is most closely related to *N. fossalis,* while *N. willamettensis* is more closely related to the remaining members of the group. The *N. leucocephala* group and *N. intertexta,* its closest extant

relative (Spencer and Porter 1997), are unique within *N.* sect. *Navarretia* for a 2-lobed (versus 3-lobed) stigma (also derived independently in *N.* sect. *Mitracarpium,* but nowhere else in the family) and are unique within the genus for their reduced corolla venation (one instead of three veins at base of corolla lobe; Spencer and Porter 1997).

The earliest collection of *N. willamettensis* known to us was made in 1922 by L. R. Abrams, who left the specimens determined only as "*Navarretia.*" Later collections (five known to us) by other workers were referred to *N. intertexta* or *N. leucocephala* subsp. *minima.* The earliest collection of *N. saximontana* known to us was in 1839 from near Devil's Lake, North Dakota, by C. A. Geyer. Collections of this species have generally been referred to *N. intertexta* subsp. *propinqua* or, less frequently, to *N. leucocephala* subsp. *minima.* Table 1 lists several characters differentiating *Navarretia willamettensis, N. saximontana, N. intertexta,* and *N. leucocephala* subsp. *minima.*

Navarretia willamettensis Stanley C. Spencer, sp. nov. (Fig. 1).—TYPE HERE DESIGNATED: USA, Oregon, Benton Co., SW Corvallis, 1.1 miles S of US Hwy 20 along Brooklane Drive, center of vernal pool in a field, T12S R5W S10, elevation 66 m, 11 Jul 1979, Richard R. Halse 2006 (holotype, OSC; isotypes, ARIZ, CAS).

Ab *Navarretia intertexta* (Benth.) Hook. corolla calyce inclusa, filamentis 0.2–1.1 mm longis et 0.1–0.6 mm sub sinubus corollae affixis differt. Ab *Navarretia leucocephala* Benth subsp. *minima* (Nutt.) A. G. Day calyce 6.3–8.0 mm longo, corolla dilute purpurea et polline sulphureo differt.

Annual, 3–16 cm tall and wide, the primary head caulescent, generally with 1–20 smaller heads at the tips of ascending lateral branches. Stem and

TABLE 1. SOME DISTINGUISHING MORPHOLOGICAL FEATURES OF *N. INTERTEXTA, N. SAXIMONTANA, N. WILLAMETTENSIS,* AND *N. LEUCOCEPHALA* SUBSP. *MINIMA*. All measurements are in mm.

Feature	*N. intertexta*	*N. saximontana*	*N. willamettensis*	*N. leucocephala* subsp. *minima*
Number of primary lobes of upper leaf	6–13	5–7	9–13	4–10
Calyx length	5.8–12	(5.6)6.0–8.0	6.3–8.0	4.6–6.0
Calyx lobe (longest) length	3.0–7.5	3.0–5.0	3.0–4.5	1.2–2.2
Style length	3.6–10	1.9–3.0(3.4)	2.7–3.7	2.2–3.9
Corolla relative to calyx	exserted	included	included	included to slightly exserted
Corolla color	white or pink to pale blue	white or pink to pale blue	pink to lavender	white
Stamen filament length	1.6–4.0	0.6–1.1	0.2–1.1	0.4–1.0
Distance from filament base to corolla lobe sinus	0.6–2.0	0.6–1.1	0.1–0.6	0.2–0.4(0.6)
Stamen position relative to corolla throat	exserted beyond corolla lobe tips	included or exserted, but not to corolla lobe tips	exserted, but not to corolla lobe tips	variously exserted
Pollen color	orange-yellow	orange-yellow	pale yellow	cream

branches green to reddish brown, puberulent. Cotyledons linear. Lower leaves opposite or alternate with linear segments, glabrous to puberulent, 10–50 mm long, with up to 13 entire or branched lobes. Upper leaves alternate, acerose, 10–22 mm long; the rachis puberulent and 4–10 mm long; the primary lobes 9–13, more or less glabrous, the lowermost often simple, the remainder (including the terminal lobe) 2–5-branched. Outer bracts similar to upper leaves but 9–13 mm long; the rachis 4–5 mm long and widened toward the base, the primary lobes (5)9–11. Inner bracts progressively smaller, with fewer lobes. Heads 12–25 mm wide, of 3–50 subsessile flowers. Calyx 6.3–8.0 mm long; the tube membranous and glabrous to gland-dotted or rarely puberulent between ribs, 2.3–3.5 mm long,

with 3–4-celled unbranched trichomes at orifice and along ribs; the lobes 5, glabrous, acerose, the two longest lobes 3.0–4.5 mm and often 2–3 pronged, the three shorter lobes 2.2–3.2 mm and simple. Corolla funnelform, pink to lavender, 4.7–6.5 mm long, exceeding the shortest but not longest calyx lobes; the limb 1.8–2.8 mm wide; the lobes oblong, 0.7–1.5 mm long, each with a single unbranched vein. Stamen filaments 0.2–1.1 mm long and inserted 0.1–0.6 mm below sinuses; the anthers exserted from throat but not to tips of the corolla lobes; the pollen pale yellow. Pistil 4.0–5.0 mm long; the ovary oblong, 2-celled; the style 2.7–3.7 mm long; the stigma 2-lobed, often exserted from corolla before anthesis, but finally included in corolla throat. Capsule 2.3–3.0 mm long, membranous, remaining in the dried heads and rupturing with autumn rains as the seed coat fibers imbibe water and expand. Seeds 2–6, brown, ovoid-angular, 1.3–2.0 mm long, reticulate-pitted, mucilaginous when wet.

Paratypes. USA, Oregon, Benton Co.: wetland prairie at confluence of Frazier and Jackson Creeks, N city limits of Corvallis, E of Hwy 99W, T11S, R5W, S13, in dried clay, in vernal pools, 29 Jul 1978, *Chambers 4541* (OSC); clay flats at end of Brook Lane, S of Corvallis, T12S, R5W, S10, in center of dried pools, in cracked bare mud, 3 Jul 1979, *Chambers 4563* (OSC); SW Corvallis, 1.1 mi S of U.S. Hwy 20 along Brooklane Drive, center of vernal pool in a field, 11 Jul 1979, *Halse 2006* (OSC); McFadden Pond, 12 mi S of Corvallis, ditchbank along road, 25 Jun 1952, *Clarkson s.n.* (OSC); Junction City to Corvallis, 5 Jul 1922, *Abrams 8729* (POM, RM); NW Corvallis at S end of Jackson-Frazier Wetlands, in swale, 9 Sep 1995, *Spencer 595-11, 61c-7* (RSA, MARY). Lane Co.: McKenzie Hwy, 6 mi E of Springfield, dried ground, 15 Jun 1934, *Andrews 137* (ORE).
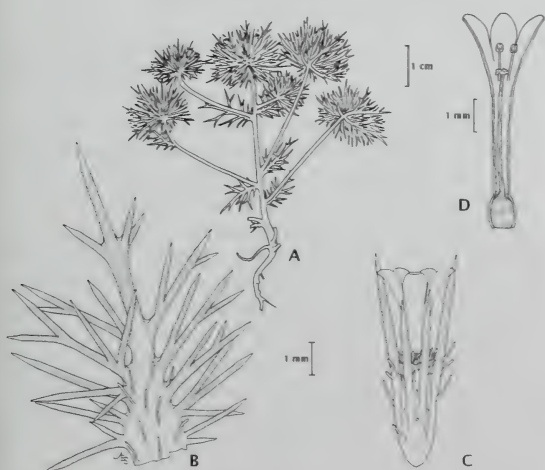
FIG. 1. *Navarretia willamettensis*. A. Habit. B. Outer bract, adaxial view. C. Flower. D. Corolla, longitudinal section, with pistil and stamens. Based on: A, *Halse 2006*; B–D, *Spencer 61c-7*.
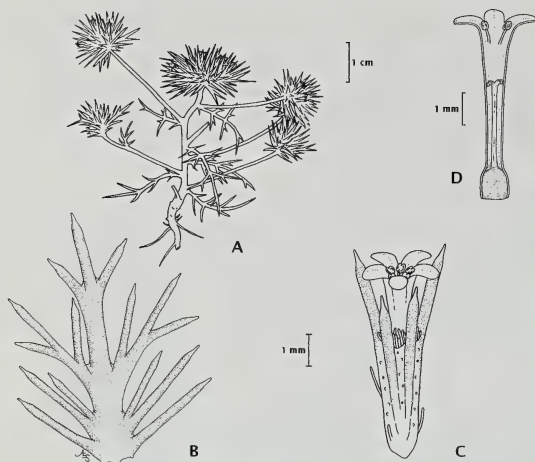
Fig. 2. *Navarretia saximontana.* A. Habit. B. Outer bract, adaxial view. C. Flower. D. Corolla, longitudinal section, with pistil and stamens. Based on *Spencer and Spencer 57V-11.*

Ecology and distribution. Navarretia willamettensis inhabits vernal pools and similar ephemeral wetlands. It flowers as the standing water recedes and the soil begins to dry between mid June and mid July. *Navarretia willamettensis* is apparently restricted to the Willamette Valley from Corvallis south to Eugene and Springfield, an area of about 1000 km² of Benton and Lane Counties in western Oregon. *Navarretia intertexta* subsp. *propinqua* and *N. leucocephala* subsp. *minima,* two of the taxa previously confused with *N. willamettensis,* are known in Oregon only east of the crest of the Cascade Range—a major geographical boundary in the Oregon flora—at a shortest distance of about 100 km from the Willamette Valley. *Navarretia intertexta* subsp. *intertexta* has a geographical range encompassing that of *N. willamettensis,* but is infrequently found in vernal pools (Spencer and Rieseberg 1998).

Navarretia saximontana Stanley C. Spencer, sp. nov. (Fig. 2).—TYPE HERE DESIGNATED: USA, Utah, Garfield Co., Dog Valley, 2.1 mi N of Redcedar Spring turnoff on Dog Valley Rd, T32S R5W S5 NE ¼ of NW ¼, 2275 m, in ephemeral lake, 31 July 1995, Spencer and Spencer 57V-11 (holotype: RSA; isotypes BRY, CAS, ORE, UC, US).

Ab *Navarretia intertexta* (Benth.) Hook. stylo 1.9–3.4 mm longo, corolla calyce inclusa, filamentis 0.6–1.1 mm longis differt. Ab *Navarretia leucocephala* Benth subsp. *minima* (Nutt.) A. G. Day lobo calycis maximo 3–5 mm longo, filamentis 0.6–1.1 mm sub sinubus corollae affixis et polline vitellino differt.

Annual, 2–12 cm tall and wide, the primary head caulescent, generally with 1–40 smaller heads at the tips of spreading or ascending lateral branches. Stem and branches green to reddish brown, puberulent to glandular-puberulent. Cotyledons linear. Lower leaves opposite or alternate with linear segments, glabrous to puberulent, 10–30 mm long, with up to 7 entire or branched lobes. Upper leaves alternate, acerose, 9–30 mm long; the rachis glabrous to puberulent or glandular-puberulent and 3–10 mm long; the primary lobes 5–7, glabrous, the lowermost often simple, the remainder (including the terminal lobe) generally 2–4-branched. Outer bracts similar to upper leaves but 7–12 mm long; the rachis 1.5–4 mm long and widened toward the base, the primary lobes 5–7. Inner bracts smaller, with fewer lobes. Heads 12–22 mm wide, of 3–50 subsessile flowers. Calyx (5.6)6.0–8.0 mm long; the tube membranous and glabrous to gland-dotted or rarely puberulent between ribs, 2.3–3.3 mm long, with 3–4-celled unbranched trichomes at orifice and along ribs; the lobes 5, glabrous, acerose, the two longest lobes 3.0–5.0 mm and occasionally 2–3 pronged, the three shorter lobes 1.5–3.0 mm and simple. Corolla funnelform, white or pink to pale blue, 4.0–6.2 mm long, not exceeding longest calyx lobes; the limb 2–3 mm wide; the lobes oblong, 0.5–1.1 mm long, each with a single, generally unbranched vein. Stamen filaments 0.6–1.1 mm long and inserted 0.6–1.1 mm below sinuses; the anthers positioned at throat orifice or exserted, but not to tips of corolla lobes; the pollen orange-yellow. Pistil 3.1–4.8 mm long; the ovary oblong, 2-celled; the style 1.9–3.0(3.4) mm long; the stigma 2-lobed, often exserted from corolla before anthesis, but finally included in corolla throat. Capsule 2.7–3.3 mm long, membranous, remaining in the dried heads and rupturing with autumn rains as the seed coat fibers imbibe water and expand. Seeds 6–12, brown, ovoid-angular, 1.2–1.5 mm long, reticulate-pitted, mucilaginous when wet.

Paratypes. CANADA, Saskatchewan: Crane Lake, Assiniboia, 20 Jun 1894, *Macoun 5545* (SASK). USA, Arizona, Coconino Co.: Ashurst Lake, ponderosa zone, near lake, 27 Jun 1980, *Lehto 24676* (RSA); Schultz Spring, San Franciso Mts Forest Reserve, elev. 2500 m., 18 Aug 1901, *Leiberg 5861* (US). Navajo Co.: 1 mi east of Pinetop, elev. 7300 ft, over-grazed meadow in *Pinus ponderosa* forest, 25 Jul 1946, *Parker 6071* (RSA, ARIZ). Colorado, Jackson Co.: 8 mi W of Hebron in North Park, low meadow, elev 9000 ft, 15 Aug 1898, *Shear & Bessey 3923, 3924* (RM, US, UTC). Idaho, Bingham Co.: NW end of Sheep Mt., 38 air mi N of Soda Springs, open areas of grassy meadow, elev 6700 ft, 15 Jul 1971, *Holmgren & Marttala 5433* (CAS, US, UTC). Teton Co.: Victor, bed of a dry slough, 11 Jul 1901, *Merrill & Wilcox 1246* (RM, US). Montana, Cascade Co.: Sand Goulee, 28 Jul 1887, *Anderson s.n.* (OSC, RM); Glacier Co.: Vicinity of Glacier Park Station, dried-up pool, 16 Aug 1919, *Standley 17730* (US); Powell Co.: 10

mi NE of Helmville, edge of pothole in sagebrush flat, 1 Jul 1948, *Hitchcock 17896* (COLO, POM, RM, RSA, US, UTC). North Dakota, Hettinger Co.: Mott, low places in prairie, 20 Jul 1937, *Meisener s.n.* (US). Mountrail Co.: Powers Lake, rather dry roadside ditch by moist prairie, 30 Jun 1946, *Stevens 872* (US). Ramsey Co.: E of Devil's Lake, dry swamp in the open prairie, Aug 1839, *Geyer s.n.* (US). Utah, Summit Co.: 7.6 mi along Hwy 150 E of Kamas, elev. 2210 m, dry ground next to a meadow, 7 Jul 1984, *Goodrich 20811* (BRY); Wasatch Co.: 15.5 mi E (79 deg) of Heber City, Little So. Fork Provo River, elev. 7500 ft, roadway in aspen-sagebrush, 11 Aug 1981, *Goodrich 16902* (BRY). Wyoming, Carbon Co.: Fort Steele, elev 6500 ft, 25 May–Jun 10 1901, *Tweedy 4414* (US). Crook Co.: Between Alva and Aladdin, elev 4400 ft, drying margin of small cattail swamp, clayey, 12 Jul 1960, *Porter & Porter 8346* (RSA). Lincoln Co.: W slope Grayback Ridge near McCain Guard Station, Bridger Natl. Forest, elev 6880 ft, open meadow, spring edge and drying shore, 19 Jul 1979, *Shultz & Shultz 3568* (RSA, USFS, UTC).

Ecology and distribution. Navarretia saximontana inhabits margins of ponds and lakes, bottoms of ephemeral streams and pools, and wet clay flats. It flowers as the water recedes and the soil begins to dry between mid June and mid September. *Navarretia saximontana* is found in North America from the Colorado Plateau of northeastern Arizona and the Rocky Mountains of Utah and southern Idaho (including the Salmon River Mountains), northeastward (through Wyoming, Montana, western Colorado, western South Dakota, and southeastern Alberta) to central Saskatchewan (near Saskatoon) and eastern North Dakota (Devil's Lake). *Navarretia saximontana* and *N. breweri* (distinguished by its yellow flowers) are the only navarretias found east of the Rocky mountains. *Navarretia intertexta* is generally found west of the Rocky Mountains and Colorado Plateau, but its range overlaps that of *N. saximontana* in Arizona near the southwestern edge of the Colorado Plateau around Flagstaff and Mormon Lake, and perhaps also along the northern edge of the Snake River Plain in southern Idaho. *Navarretia leucocephala* subsp. *minima* is found west of the Rocky mountains in Washington, Oregon, California, Nevada, and Utah. Its geographic range most closely approaches that of *N. saximontana* in northern Utah, where the two species are separated by the western foothills of the Rocky Mountains.

Navarretia leucocephala subsp. *diffusa* C. R. Bjork, a recently described taxon from eastern Washington, is distinguished from *N. willamettensis* by its white flowers, cream-colored pollen, upper leaves with fewer than eight primary lobes, and by its geographic distribution. It it is distinguished from *N. saximontana* by its cream-colored pollen, stamen filaments inserted less than 0.3 mm from corolla lobe sinuses, seeds fewer than four, and by its geographic distribution (Table 1; Bjork 2002).

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NOTE

IDAHO FLORISTICS: L. F. HENDERSON AND HIS MISLABELED 1895 COLLECTIONS FROM THE LOST RIVER MOUNTAINS OF EASTERN IDAHO

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Abstract

University of Idaho botanist, Louis F. Henderson, surveyed central and eastern Idaho in 1895 under the auspices of the U.S. National Herbarium. His unpublished report, plant lists and journals are archived at the Smithsonian Institution, Washington DC, and his collected specimens are in the U.S. National Herbarium (US). Many of his collections, including a number of types, are labeled "Lost River Mts.," and "Salmon River Mts." A close study of his trip itinerary reveals that a number of these collections were made in today's Lemhi Range. Students of Idaho floristics are here made aware of these errors and the circumstances that led to them.

This note alerts students of Idaho floristics that geographic locations on a number of Louis F. Henderson's 1895 collections from the Lost River and Salmon River Mountains at the U.S. National Herbarium (US) do not reflect modern geographical names.

The summer of 1895, Louis F. Henderson of the University of Idaho and a student assistant made a 3-month, 1000-mile reconnaissance trip through southern and eastern Idaho at the request of Frederick V. Coville, botanist at the U.S. National Herbarium. Henderson traveled through 13 present-day Idaho counties and seven National Forests. His trip journal, plant lists, final report, and hundreds of specimens are located at the Smithsonian Institution and the U.S. National Herbarium in Washington DC (Henderson 1895).

When I examined Henderson's detailed notes at the Smithsonian Botany Library in November 2001, it became clear that an important part of his assignment was to explore the relatively unknown Lost River Mountains. Unfortunately, maps of the time did not clearly delineate the location and configuration of the range. Therefore many collections, including a number of types, from the 1895 trip are mislabeled.

Henderson, his assistant, and three horses left Moscow, Idaho, June 25, 1895, and traveled south and east through central Idaho via the Salmon and Payette River Valleys, the Boise Basin, Big Camas Prairie, Hailey and Challis making many collections along the way. By August 7, they were traveling southeast through the Big Lost River Valley along the western edge of today's Lost River Range toward present-day Arco, Idaho on the Snake River Plain. On August 9, they made their only entry through the Lost River Mountains via Arco Pass in today's Challis National Forest, between Jumpoff Peak and King Peak at the southern end of the range. They then crossed the lower Little Lost River Valley, proceeding around the southern end of the present Lemhi Mountain Range to Birch Creek.

After then heading northwest along the east slope of the Lemhi Range via Birch Creek and the Lemhi River, they reached Salmon, Idaho on August 31. On this final northwest-trending leg of their journey, they made a number of penetrations into today's southern and northern Lemhi Range under the impression that these were the Lost River and Salmon River Ranges. Their route is shown on the accompanying map (Fig. 1).

Many of Henderson's specimens at US, collected from August 9 through August 15, are labeled "Lost River Mts." Of these only those collected on August 9 at Arco Pass are actually from the Lost River Mountains. His collections from August 12 through 15 were made along Birch Creek and in the Southern Lemhi Mountains (today's Targhee National Forest). Collections dated August 16 through 21 and labeled "Salmon River Mts." were made in today's Northern Lemhi Mountains (Salmon River National Forest).

Students of Idaho floristics should be aware of L. F. Henderson's erroneous geographic names when compiling plant lists or when developing distribution maps.
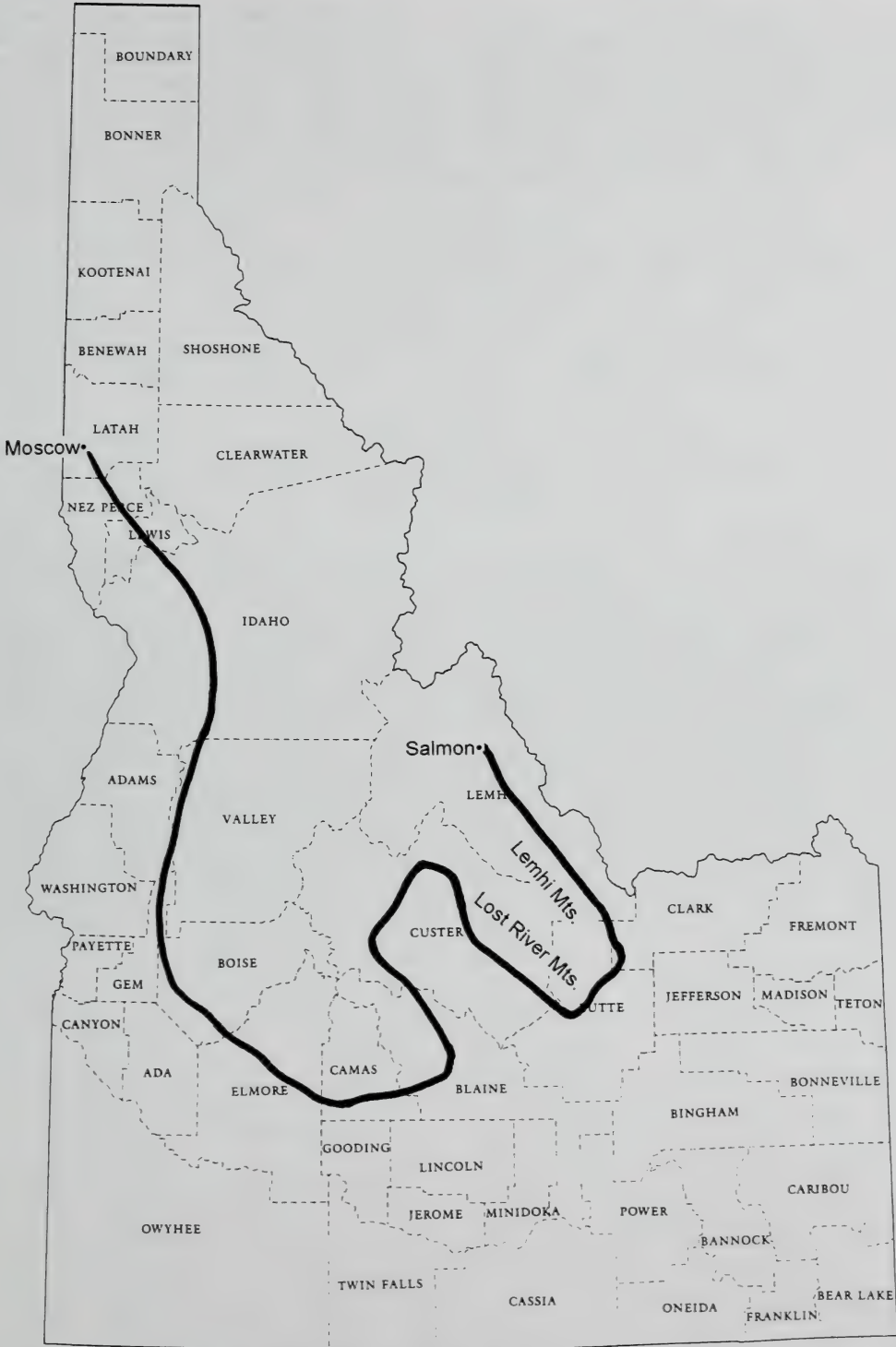
Fig. 1.   Map of Idaho showing the 1895 route of Loars F. Henderson from Moscow to Salmon with locations of today's Lost River Mts. and Lemhi Mts.

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NOTE

A COLLECTION OF *CARDARIA DRABA* (BRASSICACEAE) AND RELATED TAXA
FROM THE WESTERN UNITED STATES AND ITS IMPLICATIONS
FOR THEIR MANAGEMENT

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Presently, three species of *Cardaria* (Brassicaceae) are recognized in North America: *C. draba* (L.) Desv., *C. chalepensis* (L.) Hand.-Mazz., and *C. pubescens* (C. A. Mey.) Jarm. (Rollins 1993). Before Bellue (1933) documented their presence in North America, only *C. draba* was recognized. Mature silicles of *C. pubescens* are globose to subglobose and are densely pubescent with minute, simple trichomes (Rollins 1993). Silicles of *C. draba* (hoary cress) are cordate and usually constricted at the septum, whereas those of *C. chalepensis* are transversely oval to slightly reniform or broadly obovate, and they are not constricted at the septum (Rollins 1993). Keys and descriptions are provided by Rollins (1993) and by Mulligan and Frankton (1962). *Cardaria draba, C. chalepensis,* and *C. pubescens* have 32, 40, and 8 pairs of chromosomes, respectively (Mulligan and Frankton 1962; Mulligan and Findlay 1974; Rollins 1993). Although identifying specimens in the laboratory by number of somatic chromosomes is possible (Manton 1932; Mulligan and Findlay 1974), contrasting their morphology, especially in the field, is more convenient (Bellue 1933; Mulligan and Frankton 1962; Mulligan and Findlay 1974).

Concerning the literary record before 1933, uncertainty exists about the species to which reference has been made (Mulligan and Findlay 1974), and some weed taxonomists still do not distinguish among the three species (Mulligan and Findlay 1974). Field identification of specimens often is unreliable because all three species spend considerable time during the year as vegetative rosettes or without mature fruits (Mulligan and Findlay 1974). Although morphologically intermediate plants recognized by some (Mulligan and Frankton 1962; Mulligan and Findlay 1974; Rollins 1981) as hybrids between *C. draba* and *C. chalepensis* have

been reported without supporting data, the hybrid status of others has been confirmed cytologically (Mulligan and Frankton 1962).

The presence of *Cardaria draba, C. chalepensis,* and *C. pubescens* in the United States may have considerable economic impact. The first species is a reservoir of pathogens transmitted by many insects, and it may contribute to outbreaks of disease among important vegetable crops, including sugar beets and potatoes (Zitter 1977; Yarris 1978; Tamaki and Olsen 1979; Tamaki et al. 1982). Allelopathic properties may inhibit seed germination of other plants, including *Medicago sativa* L. (alfalfa), *Agropyron* spp. (wheatgrass), and *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) (Kiemnec and McInnis 2002). In laboratory and greenhouse experiments, shoot residues of *C. draba* inhibited seed germination and seedling growth of *Brassica oleracea* L. var. *Capitata* cv. Pronzwik (cabbage), *Daucus carota* L. cv. Natus (carrot), *Cucumis sativus* L. cv. Beithalpha (cucumber), *Cucurbita pepo* L. cv. Byrouti (squash), *Allium cepa* L. cv. Texas Early Grana (onion), *Capsicum annuum* L. cv. Red Common (pepper), and *Lycopersicon esculentum* Mill cv. Special Black (tomato) (Qasem 2001). *Cardaria pubescens* is reported as a source of inoculum for *Xanthomonas campestris,* a fungus responsible for black rot among cruciferous crops (Schaad and Dianese 1981). Of the three species, *C. chalepensis* is considered the most aggressive at colonizing new habitats (Mulligan and Findlay 1974).

To illustrate the frequency with which adequate systematic resolution is not possible in the field, specimens of *C. draba, C. chalepensis,* and *C. pubescens* from the western United States were collected (see Appendix 1). After their identification by Dr. Ihsan Al-Shehbaz (MO), they were depos-

ited either at the Missouri Botanical Garden or at the University of Georgia, Department of Botany in Athens (see Appendix 1 for the institution at which each specimen has been deposited). Of the 97 vouchered specimens, Al-Shehbaz identified 47 as *C. draba,* 22 as *C. chalepensis,* and 11 as *C. pubescens.* Seventeen of the 97 specimens were not readily identifiable; 8 are *C. chalepensis* with distinct features of *C. draba,* and they may be of hybrid origin. These intermediates possess distinctly carinate fruits, reticulate valves, or only slightly cordate fruits. Nine specimens are either *C. draba* or *C. chalepensis,* but further resolution is not possible because only young fruits are present.

Although specimens documented in this manuscript bear the generic name *Cardaria, Lepidium* also has gained increasing acceptance. Presence of indehiscent fruits has been used to distinguish *Cardaria* from *Lepidium* (Al-Shehbaz 1986; Rollins 1993), but some authors synonymized the genera because representative taxa in *Lepidium* possess tardily dehiscent or indehiscent fruits (Thellung 1906; Rich 1991). Furthermore, molecular data strongly suggest that *Cardaria* is nested within *Lepidium,* the earliest generic name of the group (Mummenhoff 1995; Brüggemann 2000), and the three species now are formally recognized as members of *Lepidium* (Al-Shehbaz et al. 2002).

Difficulty identifying immature material of *Cardaria* has significant implications for their management. Differential response of each species to a variety of herbicides is dose dependent (Jenkins and Jackman 1938; Sexsmith 1964), and anecdotal reports that herbicides are ineffective against hoary cress may simply reflect frequency of misidentification in the field (Sexsmith 1964). Biological control has been used successfully against many invasive/exotic plants in the United States, including *Euphorbia* spp. (Anderson et al. 2000), *Carduus nutans* L. (Surles and Kok 1976) and *Lythrum salicaria* L. (Wiebe and Obrycki 2001), but attempts to develop a biological control program for *Cardaria* spp. may be encumbered by inability to reconcile survey for potential agents with identity of plants from which they have been collected. Incomplete systematic resolution has been or is an obstacle to developing integrated management programs for other invasive/exotic plants, including *Euphorbia* spp. (Galitz 1980; Harvey et al. 1988; Crompton et al. 1990), *Pueraria* spp. (Jewett et al. 2003), and *Vincetoxicum* spp. (Sheeley and Raynal 1996). Any integrated management program directed against the three *Cardaria* spp. in North America will be of limited value without more convenient and reliable means of identifying specimens in the field.

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APPENDIX 1. DATA CONCERNING ACCESSIONS OF *CARDARIA DRABA* (L.) DESV., *C. CHALEPENSIS* (L.) HANDEL-MAZETTI, AND *C. PUBESCENS* (C. A. MEYER). [1] Specimens vouchered at the University of Georgia Herbarium (Department of Plant Sciences, University of Georgia, Athens) as *C. draba* (L.) Desv. and *C. chalepensis* (L.) Hand.-Maz. are vouchered at the MIssouri Botanical Garden in St. Louis as *C. draba* (L.) subsp. *draba* and *C. draba* (L.) subsp. *chalepensis* (L.) O.E. Schulz, respectively. [2] Specimens referred to as *C. draba* × *C. chalepensis* were treated by Ihsan Al-Shehbaz (Missouri Botanical Garden, St. Louis) as "'... *C. draba* subsp. *chalepensis* with distinct features of subsp. *draba* (namely either the distinctly carinate fruits, reticulate valves, or slightly cordate fruit base). It is likely that they (at least in part) (are) intermediates of possible hybrid orgin."' [3] Contact information for cooperators is included in "ACKNOWLEDGMENTS."

Voucher no.	Herbarium	Species[1,2]	State	County	Acknowledgment[3]	Date	Lat. (dd)	Lon. (dd)	El. (m)
2	GA, MO	*C. pubescens*	WY	Park	Bob Parsons	07/31/99	44.7260	-108.7583	1339
6	GA	*C. draba*	OR	Harney	Bonnie Rasmussen	08/02/99	43.5824	-119.0547	1264
7	GA	*C. draba* × *C. chal.*	OR	Harney	Bonnie Rasmussen	08/02/99	43.5871	-119.0197	1250
8	GA	*C. pubescens*	OR	Harney	Bonnie Rasmussen	08/02/99	43.5871	-119.0197	1250
11	GA	*C. draba*	OR	Malheur	Dan Sharratt	08/03/99	43.9832	-117.2344	685
12	GA, MO	*C. draba*	OR	Malheur	Dan Sharratt	08/03/99	43.9959	-117.0398	676
13	GA	*C. draba*	OR	Baker	Dan Sharratt	08/03/99	44.5903	-117.4725	815
14	GA, MO	*C. draba*	OR	Baker	Dan Sharratt	08/03/99	44.7845	-117.8095	1054
15	GA, MO	*C. pubescens*	NV	Humboldt	M. Gaffri/D. Jewett	08/04/99	41.0048	-117.7313	1347
17	GA	*C. pubescens*	NV	Humboldt	Martin Larinetta	08/05/99	40.9908	-117.6993	1334
18	GA	*C. pubescens*	NV	Humboldt	Martin Larinetta	08/05/99	40.9913	-117.7310	1309
21	GA, MO	*C. pubescens*	NV	Storey	M. Gaffri/D. Jewett	08/05/99	39.1942	-119.7758	1440
23	GA	*C. draba* × *C. chal.*	CA	San Joaquin	Ross O'Connell	08/08/99	37.7569	-121.4640	-7
24	GA	*C. draba* × *C. chal.*	CA	San Joaquin	Ross O'Connell	08/08/99	37.7567	-121.4649	-4
25	GA, MO	*C. pubescens*	CA	San Joaquin	Ross O'Connell	08/08/99	37.7732	-121.4624	-7
26	GA	*C. draba* × *C. chal.*	CA	San Joaquin	Ross O'Connell	08/08/99	37.7703	-121.4622	-8
28	GA	*C. draba*	UT	Beaver	Mark Nelson	08/10/99	38.3241	-112.9833	1546
30	GA	*C. chalepensis*	UT	Iron	Chad Reid	08/11/99	37.6684	-113.0719	1791
31	GA	*C. chalepensis*	UT	Iron	Chad Reid	08/11/99	37.7455	-113.0656	1702
32	GA, MO	*C. draba*	UT	Sevier	Mark Nelson	08/11/99	38.7544	-112.1043	1625
37	GA, MO	*C. chalepensis*	CO	Montrose	M. Gaffri/D. Jewett	08/12/99	38.5568	-107.9519	1716
40	GA, MO	*C. chalepensis*	CO	Garfield	M. Gaffri/D. Jewett	08/13/99	39.4312	-108.7882	1629
41	GA	*C. draba* × *C. chal.*	CO	Garfield	M. Gaffri/D. Jewett	08/13/99	39.5708	-108.8019	2034
43	GA, MO	*C. pubescens*	WY	Sweetwater	M. Gaffri/D. Jewett	08/13/99	42.0142	-109.4252	2004
51	GA	*C. draba*	WY	Albany	M. Gaffri/D. Jewett	08/14/99	41.1886	-105.5964	2236
52	GA, MO	*C. chalepensis*	WY	Albany	David Kazmer	08/17/99	41.3063	-105.6161	2188
53	GA	*C. chalepensis*	WY	Albany	David Kazmer	08/17/99	41.2915	-105.6335	2192
54	GA	*C. chalepensis*	WY	Albany	David Kazmer	08/17/99	41.3197	-105.6391	2206
55	GA, MO	*C. draba*	WY	Albany	David Kazmer	08/17/99	41.3132	-105.6314	2202
57	GA	*C. draba* × *C. chal.*	CO	Weld	Ron Broda	08/18/99	40.1755	-104.9738	1470
58	GA	*C. draba* × *C. chal.*	CO	Weld	Ron Broda	08/18/99	40.1732	-104.9885	1469
60	GA	*C. chalepensis*	CO	Weld	George Beck	08/18/99	40.6101	-104.9880	1526
61	GA	*C. chalepensis*	WY	Converse	Skip Lewis	08/19/99	42.7560	-105.4062	1477
64	GA	*C. chalepensis*	WY	Converse	Skip Lewis	08/19/99	42.7654	-105.4901	1541
66	GA, MO	*C. chalepensis*	WY	Converse	Skip Lewis	08/19/99	42.8680	-105.8653	1523
72	GA	*C. draba*	MT	Yellowstone	Terrie van Buren	09/16/99	45.7551	-108.5156	951
73	GA	*C. draba* × *C. chal.*	MT	Yellowstone	Terrie van Buren	09/16/99	45.8082	-108.4507	944

APPENDIX 1. CONTINUED.

Voucher no.	Herbarium	Species[1,2]	State	County	Acknowledgment[3]	Date	Lat. (dd)	Lon. (dd)	El. (m)
74	GA	C. chalepensis	MT	Yellowstone	Terrie van Buren	09/16/99	45.8454	−108.4828	982
78	GA	C. pubescens	WY	Fremont	Lars Baker	09/17/99	42.8516	−108.6902	1646
79	GA	C. draba	WY	Fremont	Lars Baker	09/17/99	42.8516	−108.6902	1646
81	GA	C. pubescens	WY	Fremont	Lars Baker	09/17/99	43.0000	−108.4167	1524
82	GA, MO	C. draba	WY	Fremont	Lars Baker	09/17/99	43.2222	−108.8111	1646
84	GA, MO	C. draba	WY	Big Horn	M. Gaffri/D. Jewett	09/17/99	44.5250	−108.3361	1311
85	GA	C. chalepensis	ND	Williams	M. Gaffri/D. Jewett	10/07/99	48.1454	−103.6463	606
130	GA	C. draba or C. chal.	UT	Cache	Steve Dewey	05/03/00	41.9081	−111.8139	1404
132	GA	C. draba	UT	Cache	Steve Dewey	05/04/00	41.7449	−111.8593	1342
133	GA	C. draba	UT	Cache	Steve Dewey	05/04/00	41.7319	−111.8701	1342
134	GA	C. draba	UT	Box Elder	Steve Dewey	05/04/00	41.7462	−111.9543	1335
135	GA	C. draba	UT	Box Elder	Steve Dewey	05/04/00	41.7852	−112.1383	1313
136	GA	C. draba or C. chal.	UT	Cache	Steve Dewey	05/04/00	41.7503	−111.8354	1367
137	GA	C. draba or C. chal.	UT	Cache	Steve Dewey	05/04/00	41.7496	−111.8388	1351
139	GA	C. draba	UT	Box Elder	Steve Dewey	05/05/00	41.7417	−112.1439	1299
140	GA	C. draba	UT	Box Elder	Steve Dewey	05/05/00	41.7111	−112.1607	1291
141	GA	C. draba	UT	Box Elder	Steve Dewey	05/05/00	41.6985	−112.1621	1296
142	GA	C. draba	UT	Box Elder	Steve Dewey	05/05/00	41.7018	−112.1232	1309
143	GA	C. draba	UT	Box Elder	Steve Dewey	05/05/00	41.7189	−112.1654	1301
144	GA	C. draba	UT	Box Elder	Steve Dewey	05/05/00	41.7086	−112.1734	1309
146	GA	C. draba	UT	Box Elder	Steve Dewey	05/06/00	41.7091	−112.2288	1306
147	GA	C. draba	UT	Box Elder	Steve Dewey	05/06/00	41.7099	−112.2069	1300
148	GA	C. draba	UT	Box Elder	Steve Dewey	05/06/00	41.6958	−112.2261	1293
149	GA	C. draba or C. chal.	UT	Box Elder	Steve Dewey	05/06/00	41.6302	−112.2375	1287
150	GA	C. draba	UT	Box Elder	Steve Dewey	05/06/00	41.6317	−112.2462	1301
151	GA	C. draba	UT	Box Elder	Steve Dewey	05/06/00	41.5618	−112.1615	1273
152	GA	C. draba	UT	Box Elder	Steve Dewey	05/06/00	41.5097	−112.1071	1269
155	GA	C. draba	UT	Weber	Steve Dewey	05/07/00	41.1733	−112.0157	1347
156	GA	C. draba or C. chal.	UT	Davis	Steve Dewey	05/07/00	41.1353	−112.0262	1379
157	GA	C. draba or C. chal.	UT	Davis	Steve Dewey	05/07/00	41.1095	−112.0222	1349
158	GA	C. draba	UT	Davis	Steve Dewey	05/07/00	41.0446	−111.9501	1295
159	GA	C. draba	UT	Davis	Steve Dewey	05/07/00	41.0813	−111.9124	1447
160	GA	C. draba	UT	Morgan	Steve Dewey	05/07/00	41.0825	−111.7291	1493
161	GA	C. draba	UT	Salt Lake	Steve Dewey	05/07/00	40.7742	−111.7084	1787
162	GA	C. draba	UT	Salt Lake	Steve Dewey	05/07/00	40.3298	−111.6184	1519
163	GA	C. draba	UT	Utah	Steve Dewey	05/07/00	40.2825	−111.6592	1411
164	GA	C. draba	UT	Utah	Steve Dewey	05/08/00	40.1895	−111.6490	1354
165	GA	C. draba	UT	Utah	Steve Dewey	05/08/00	40.1467	−111.6082	1377
166	GA	C. draba or C. chal.	UT	Utah	Steve Dewey	05/08/00	40.1011	−111.6556	1381
167	GA	C. draba	UT	Utah	Steve Dewey	05/08/00	39.9855	−111.7677	1455
168	GA	C. draba	UT	Utah	Steve Dewey	05/08/00	39.9524	−111.9328	1387

APPENDIX 1. CONTINUED.

Voucher no.	Herbarium	Species[1,2]	State	County	Acknowledgment[3]	Date	Lat. (dd)	Lon. (dd)	El. (m)
169	GA	C. draba	UT	Juab	Steve Dewey	05/08/00	39.9622	-112.0986	1972
170	GA	C. draba or C. chal.	UT	Toole	Steve Dewey	05/08/00	39.9622	-112.0986	1972
171	GA	C. draba or C. chal.	UT	Toole	Steve Dewey	05/08/00	40.0750	-112.3840	1730
172	GA	C. draba	UT	Toole	Steve Dewey	05/08/00	40.1605	-112.4307	1592
173	GA	C. draba	UT	Toole	Steve Dewey	05/08/00	40.3013	-112.4026	1516
174	GA	C. draba	UT	Toole	Steve Dewey	05/08/00	40.4396	-112.3708	1526
175	GA	C. draba	UT	Toole	Steve Dewey	05/08/00	40.5657	-112.2942	1443
176	GA	C. draba	UT	Toole	Steve Dewey	05/08/00	40.6850	-112.2641	1281
177	GA	C. chalepensis	UT	Salt Lake	Steve Dewey	05/08/00	40.7641	-112.0631	1280
180	GA	C. chalepensis	WA	Benton	M. Gaffri/D. Jewett	06/08/00	46.2508	-119.7369	231
181	GA	C. chalepensis	WA	Yakima	M. Gaffri/D. Jewett	06/09/00	46.5707	-120.4839	279
182	GA	C. pubescens	WA	Yakima	M. Gaffri/D. Jewett	06/09/00	46.7393	-120.7402	445
183	GA	C. chalepensis	WA	Yakima	M. Gaffri/D. Jewett	06/09/00	46.6857	-120.4781	351
184	GA	C. chalepensis	WA	Yakima	M. Gaffri/D. Jewett	06/09/00	46.3712	-120.3205	200
185	GA	C. chalepensis	WA	Yakima	M. Gaffri/D. Jewett	06/09/00	46.2925	-120.1833	188
186	GA	C. chalepensis	WA	Yakima	M. Gaffri/D. Jewett	06/09/00	46.1869	-119.8962	185
187	GA	C. chalepensis	MT	Powell	M. Gaffri/D. Jewett	06/11/00	46.3750	-112.7333	1402
188	GA	C. draba	MT	Deer Lodge	M. Gaffri/D. Jewett	06/11/00	46.0958	-112.8125	1508
189	GA	C. chalepensis	MT	Jefferson	M. Gaffri/D. Jewett	06/11/00	45.8792	-112.0958	1373

NOTE

SPARTINA FOLIOSA (POACEAE)—A COMMON SPECIES ON THE ROAD TO RARITY?

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ABSTRACT

Spartina alterniflora Lois. (smooth cordgrass), native to salt marshes of the eastern US and Gulf coasts was introduced into San Francisco Bay for salt marsh restoration in the 1970s. It subsequently hybridized with the California native *S. foliosa* Trin. Many of the *S. alterniflora* × *S. foliosa* hybrids are highly fit, with flowering periods that overlap the parental species, and profuse pollen and seed production. Hybrid pollen can sire seed on the native; seed which then disperses by floating on the currents of the Bay. The fittest hybrids are taller, have denser culms, and denser deeper roots than either parental species, and hybrids overgrow naturally open mud and the native salt marsh species. As primary interspecific crosses of the pure parental species are rare, we posit that the hybrid swarm spreads by backcrossing and interbreeding of fit hybrids rather than by primary crossing of pure parental species. The combination of reproductive and ecological superiority is leading inexorably to the conversion of native salt marsh to tall, dense swards of hybrid cordgrass, with deleterious effects upon native species, and on navigation, flood control and other human uses of the San Francisco estuary. Native *S. foliosa* is virtually absent in marshes where hybrids have grown longest in San Francisco Bay. A few hybrids have colonized north of the Golden Gate, in Marin Co. and San Pablo Bay. Floating seed has the potential to export hybrids and immediately threaten *S. foliosa* throughout its range in Northern California. We conclude that this suite of characters (reproductive and ecological vigor combined with tidally dispersed seed), will drive rampant spread of hybrids and ultimately could lead to the extirpation of *S. foliosa* in the San Francisco estuary.

In the 1970s the United States Army Corps of Engineers (USACE) conducted two restoration projects that established populations of the alien *Spartina alterniflora* in the San Francisco Bay. The first project was near the mouth of New Alameda Creek near the town of Fremont in the south Bay. Dredge spoil was deposited into a salt pond (Pond 3) in 1973, which was opened to tidal action in October 1975 (USACE 1976). Although a research team recommended the use of California native species for marsh reclamation, *S. alterniflora* was planted into the Pond 3 restoration site (Faber 2000).

The second project was on Alameda Island. A pre-construction report (USACE 1978) called for 9,800 plants of *S. alterniflora* and 3,000 plants of *S. foliosa* to be planted southwest of Willow Ave. in Alameda, allowing comparison of the substrate holding capacity of these species.

Over 80% of tidal marshes in the San Francisco estuary were lost during the last century (MacDonald 1977). Building new marshes and protecting beaches from tidal erosion are worthy endeavors (USACE 1978). However, the introduction of *S. alterniflora* and its subsequent hybridization with *S. foliosa* could lead to the extirpation of *S. foliosa* in San Francisco Bay.

Spartina foliosa Trin.

Spartina foliosa (California cordgrass) is the only native *Spartina* species on the North American Pacific coast (Mobberly 1956). It grows at the low fringe of native terrestrial vegetation on estuarine shorelines throughout its range from Baja California to Bodega Bay, CA. from approximately mean sea level to mean high water tidal elevations (Atwater and Hedel 1976). *Salicornia* spp. dominates higher in these salt marshes. *Spartina foliosa* plays a critical role in habitat structure (Zedler 1996), productivity, and geomorphology of Pacific salt marshes (Gabet 1998). It is usually less than 1 m tall with diffuse stems and roots that serve as habitat and foraging areas for native invertebrates, fish, and shorebirds. Tidal immersion likely inhibits growth farther down the tidal gradient (Hinde 1954; Mahall and Park 1976). As a result of its short stature and relatively sparse growth, *S. foliosa* does not accrete sediment aggressively, and the borders of native salt marshes remain high on the intertidal plane. This leaves vast expanses of open mud at low tide as the primeval condition of Pacific salt marshes. In years of high rainfall, *S. foliosa* seed can germinate on the open mud at the upper end of the tidal gradient and grow into circular colonies several meters in diameter in subsequent years (personal observation). Until the arrival of *S. alterniflora* in San Francisco Bay, *S. foliosa* was the only emergent vascular plant on the

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lower salt marsh border, and it dominated thousands of hectares of salt marsh in San Francisco Bay (Goals Project 1999).

The large populations of *S. foliosa* in San Francisco Bay and in Baja California have smaller disjunct populations in the isolated estuaries in between. A gap in distribution extends from the south end of San Francisco Bay to Mugu Lagoon, Ventura County. *Spartina foliosa* disappears from estuaries with tidal inlets that are or were periodically closed (Zedler 1982) such as Morro Bay and Elkhorn Slough. North of San Francisco Bay, *S. foliosa* grows in Bolinas Lagoon and in Drakes Estero on Pt. Reyes; the largest stands are in the mouth of Limantour Estero and at the head of Schooner Bay. The population of *S. foliosa* in Tomales Bay was very small in 1988 (Strong personal observation). During the past decade, *S. foliosa* spread rapidly on the mudflats at the southernmost end of Tomales Bay and covered dozens of hectares by the end of the century (Ayres, Baye personal observation). It is absent from the large Walker Creek delta and the rest of northern Tomales Bay. *Spartina foliosa* was absent from Bodega Bay in the 1960s (Barbour et al. 1973) but a small population has been in the south end of the Bay since the 1970s (Abresch 1975).

The largest populations of *S. foliosa* in the San Francisco estuary are in south San Francisco Bay and San Pablo Bay on soft sediments. Recruitment from seed has been rapid in restored tidal salt marshes at Napa Marsh (Pond 2A) and outer Bair Island. Narrow fringing populations grow at the low edge of salt marsh vegetation on the banks of tidal creeks in south San Francisco Bay, San Pablo Bay, the Petaluma River, and the Napa River. Small populations grow in a few places in the constantly brackish (in the dry season) and fresh waters (in the rainy season) of Suisun Bay (Brenda Grewell personal communication). In the Napa River mouth, *S. foliosa* disappears with the high fresh water flows of wet winters. We have observed various tules (*Scirpus* spp.) in these places following the disappearance of *S. foliosa*.

The Hybrid Swarm of *S. alterniflora* × *S. foliosa*

Although relatively short and far less aggressive in growth, *Spartina foliosa* is closely related to *S. alterniflora*, the dominant salt marsh cordgrass of the Atlantic and Gulf of Mexico coasts (Mobberly 1956; Chapman 1964). *Spartina alterniflora* is much denser and taller than *S. foliosa*, and grows vigorously at higher and lower elevations in the salt marsh than *S. foliosa* (Callaway and Josselyn 1992). The first studies in San Francisco Bay concluded that the physical robustness of *S. alterniflora* and its ability to overgrow *S. foliosa* would lead to the competitive elimination of *S. foliosa* (Callaway and Josselyn 1992). Then, molecular systematic studies found that the two species had hybridized in San Francisco Bay (Daehler and Strong 1997).

Subsequently we discovered that the native was almost absent at the USACE restoration sites at Alameda Creek and Alameda Island; those marshes were dominated by hybrids and *S. alterniflora* (Ayres et al. 1999). Hybrids also can invade and take over marshes of pure native *S. foliosa*. For example, on the shore south of the San Lorenzo Creek, coverage of hybrids increased at the expense of native *S. foliosa* 8-fold in three years, from 5% in 1997 (Ayres et al. 1999), to 42% in 2000 (Ayres and Strong personal observation) owing to lateral growth of plants.

Transgressive traits are those that are more extreme in hybrids than in both parental species (Rieseberg et al. 1999). Unlike the hybrid vigor that arises due to heterosis, transgressive traits are due to combinations of loci from the parental species and can be heritable. To examine the magnitude of differences in traits between hybrids and the parental species, we gathered data from various sources (Zaremba 2001; Ayres et al. in press; Ayres and Strong personal observation). Traits were grouped into characters of early life stages (i.e., seed germination, and seedling survival and growth), characters of mature plants (i.e., stature and biomass), and reproductive characters (i.e., inflorescence size, seed and pollen production, etc.). We employed a hybrid index that condensed our molecular analyses in order to categorize hybrids and parental genotypes; plants with all the molecular traits of *S. alterniflora* were regarded as pure *S. alterniflora,* and plants with none of the molecular traits of *S. alterniflora* were regarded as pure *S. foliosa* (see Ayres et al. 1999). Hybrids were placed into categories based on the proportion of *S. alterniflora* molecular traits they possessed. To facilitate comparisons among traits, raw data for each trait were ranked relative to the largest measurement; e.g., the category with the tallest plants was ranked at 1.0; categories with shorter plants received a proportionally smaller rank.

Many cordgrass hybrid plants have transgressive traits in San Francisco Bay; some hybrids exceed both parental species in every trait that we have measured (Table 1): germination, seedling survival, stature, lateral expansion, biomass, as well as the gamut of traits affecting sexual reproduction (inflorescence length, seedset, seed viability, and pollen production). For example, comparing rates of lateral expansion, at the Cogswell marsh in Hayward many hybrids increased in area ca 2.5 fold, and a few more than 4 fold, more rapidly than the few remaining *S. foliosa* during 1999–2000 (Zaremba 2001).

Initially, we believed that primary interspecific hybridization between pure parental species was the driving force of hybrid spread. Our hypothesis was that in every generation the prodigious pollen output of *S. alterniflora* swamped *S. foliosa* flowers to produce a continual stream of F1 hybrids (Anttila et al. 1998).

However, we have subsequently found no F1s

TABLE 1. PLANT LIFE HISTORY AND PERFORMANCE TRAITS TRANSFORMED INTO RANKED VALUES (=VALUE/MAXIMUM VALUE) (ORIGINAL DATA FROM [1] AYRES AND STRONG UNPUBLISHED, [2] AYRES ET AL. IN PRESS; [3] ZAREMBA 2001). Hybrid category is based on the percent of species-specific marker states consistent with *S. alterniflora*; *S. foliosa* having 0%, and *S. alterniflora* having 100% of the molecular traits, respectively.

		Genetic background					
			Hybrid Category				*S. alterni-flora*
Trait	*S. foliosa*	1–20	21–40	41–60	61–80	81–99	
YOUNG PLANTS[1]							
germination	0.96	0.81	0.54	0.88	0.77	1.00	0.83
seedling survival	0.77	1.00	0.78	0.77	0.76	0.73	0.87
seedling growth (by mother)	0.75	0.95	0.66	1.00	0.94	0.96	0.89
seedling growth (by seedling)	0.70	0.95	0.95	0.85	1.00	0.90	0.83
Rank mean young plants	**0.86**	**1.00**	**0.79**	**0.94**	**0.93**	**0.96**	**0.93**
Mature plants							
greenhouse-grown plants[2]	0.54	0.34	0.63	0.80	1.00	0.90	0.67
field (*in situ*) plants[3]	0.78	0.76	0.92	1.00	0.94	0.92	0.74
Rank mean mature plant size	**0.68**	**0.56**	**0.80**	**0.92**	**1.00**	**0.94**	**0.73**
SEXUAL REPRODUCTION[3]							
inflorescence length	0.64	0.72	0.79	0.94	0.74	1.00	
seed set	0.64	0.93	0.49	1.00	0.25	0.56	
pollen viability	0.20	0.36	0.78	1.00	0.86	0.79	
maximum flowering	1.00	0.85	0.83	0.83	0.69	0.39	0.11
mean seed prod'n/m^2	0.34	1.00	0.16	0.62	0.03	0.31	0.00
mean pollen prod.'n/m^2	0.06	0.34	0.33	0.62	0.07	1.00	0.00
Rank mean sexual production	**0.30**	**1.00**	**0.36**	**0.92**	**0.07**	**0.98**	**0.00**
Rank mean clonal spread[3]	**0.41**	**0.64**	**1.00**	**0.84**	**0.72**	**0.86**	**0.64**
Overall mean rank	**0.60**	**0.86**	**0.79**	**0.98**	**0.73**	**1.00**	**0.62**

among the hybrids in the Bay. This implies that primary interspecific hybridization is rare and that the loss of *S. foliosa* is due to backcrossing. Thus, we hypothesize that hybrids (rather than *S. alterniflora*) pollinate *S. foliosa*, other hybrids, and the alien parental species to produce large numbers of genetically heterogenous hybrid seed (Anttila et al. 2000). Our genetic evidence (Ayres et al. 1999) of a "hybrid swarm" supports this conjecture.

Pure interspecific crosses are rare because *S. alterniflora* and *S. foliosa* flower at different times of the year (Ayres and Strong personal observation). There are, as well, other barriers to prevent primary interspecific hybridization. We have had only limited success in creating a F1 through hand crossing with parental species manipulated to flower simultaneously (Ayres and Strong personal observation). While the flowering periods of the two parental species hardly overlap, peak flowering of some hybrids occurs between the parental species and overlaps broadly with both, facilitating the secondary backcrossing. Finally, seed set by *S. foliosa* and sired by hybrids is quite fertile (Ayres and Strong personal observation).

We conclude that this suite of reproductive characters (intermediate flowering, more pollen production than parental species, and highly fertile hybrid seed (Table 1) confers high fitness on hybrids in reproductive characters. The logic of this scenario is that the process driving the spread of the hybrid

swarm is backcrossing of transgressively fit hybrids rather than primary crossing of pure parental species. In combination with high vegetative fitness, this results in unchecked spread. Backcrossing hybridization is a process of positive feedback that can readily result in elimination of *S. foliosa* where hybrids grow without control.

While genetic assimilation, the loss of a species due to hybridization, can cause the extinction of rare species (Rieseberg 1991; Rymer and Simberloff 1996), it generally has not been perceived to be a major threat to common, wide ranging species, like *S. foliosa*. The magnitude of the threat posed by genetic assimilation to common species was illustrated in two recent theoretical analyses. Epifanio and Philipp (2001) examined the population genetic composition through time of two-species admixtures as a function of the initial frequencies of the two species, the strength of assortative mating, and the fitness of hybrids. Unless there was no interspecific hybridization, hybrid fitness exceeding 0.15 (where maximum fitness was standardized to 1.0) always resulted in the genomic extinction of both species, with rare species going extinct faster than more common species. Genomic extinction was defined as the extinction of taxa expressing monophyletic genotypes. We ran their model estimating *Spartina* species and hybrid fitness values from our overall rankings of hybrids and parental species (Table 1). Simulating the introduction of a single individual of *S.*

alterniflora into a native marsh resulted in genomic extinction of *S. foliosa* in six generations. Introduction of a hybrid into a native marsh resulted in extinction in five generations. Increasing the proportion of non-native genotypes hastened the extinction of *S. foliosa* by one generation. In all simulations, both species—*S. foliosa* and *S. alterniflora*—were replaced by a hybrid swarm.

A second theoretical analysis used an individual-based plant life history approach examining the importance of seed and pollen production, selfing rate, and the competitive ability of seedlings (Wolf et al. 2001). Their analysis predicted that *S. foliosa* would become extinct in an invaded population within 3 to 20 generations owing to low fertility and competitive ability relative to *S. alterniflora*. The linear nature of the shoreline and its marshes as well as long-lived clones of the native would likely slow the progress of total elimination in the Bay forecast from their model. The local extinction and replacement by hybrids of *S. alterniflora*, as well as the native, was also predicted when hybrids had high fertility and competitive ability, and *S. alterniflora* numbers were low. Although this model assumed ready production of F1 hybrids, which we now know does not occur in cordgrass in San Francisco Bay, the qualitative result of local extinction of the native in marshes invaded by hybrids is logically sound given the superior siring and competitive abilities of hybrids (Table 1; L. Rieseberg personal communication). Without control of *S. alternflora* and hybrids, these models, as well as our findings, predict the extirpation of *S. foliosa* in the San Francisco estuary.

Spread By Floating Seed

Carried by tidal currents, floating seed has spread hybrids of *S. alterniflora* and *S. foliosa* extensively through the southern end of San Francisco Bay (Ayres et al. in press). Hybrids have also colonized at sites north of the Golden Gate. In 2000 and 2001 we discovered several large, isolated plants at Richardson Bay, Corte Madera Creek, and near Pt. San Rafael on the west shore and as far north as Pt. Pinole on the east shore (Ayres et al. in press). As hybrid populations increase, they will export more seed and colonize new places in San Francisco Bay and San Pablo Bay. Hybrid seed can also float out through the Golden Gate. Seed of *S. alterniflora* has floated out of Willapa Bay, WA and colonized estuaries as many as 100 km to the north of the source population (Sayce et al. 1997). We do not know the source of the large *S. alterniflora* plant found growing in the Bolinas Lagoon, or that of the three large plants found growing in Drake's Estero, in Pt. Reyes National Seashore during 2002 (Katy Zaremba, Shannon Klohr, Patrick McIntire personal communications); they could have arisen from seed of *S. alterniflora* that floated out of the Golden Gate. It appears that no hybrids have yet formed from these introductions.

Ecosystem Effects of Hybrids

Other Spartina invasions provide examples of the ecological consequences of non-native cordgrasses. The case of *Spartina anglica* C. E. Hubbard (English cordgrass) provides one example. This species is a hybrid of *S. alterniflora* that has spread far beyond the range of the native European cordgrass parent *S. maritima*. It has altered estuaries greatly in Europe, Puget Sound, Australia, New Zealand, and China. It overgrows open mud and accretes sediment, transforming tidal mudflat into elevated, dense, monotypic marsh (Partridge 1987; Thompson 1991). *Spartina anglica* is an allopolyploid species that is unable to backcross to its parental species and thus does not pose a threat to the genetic integrity of *S. maritima*. Another example is *S. alterniflora* introduced to Willapa Bay, WA. This invasion has caused large-scale losses of intertidal mudflat and oyster-farmed tidelands, and spurred major, very expensive eradication efforts (Mumford et al. 1990; Wu et al. 1999). Habitat characteristics make Pacific estuaries of North America quite vulnerable to invasion and severe modification by several species of *Spartina* (Daehler and Strong 1996) and hybrid *S. alterniflora* × *S. foliosa* is equally or more invasive than these congeneric invaders.

Conclusions

It is reasonable to assume that, without control, hybrids of *S. alterniflora* × *S. foliosa* will continue rampant spread through San Francisco Bay salt marshes. *Spartina* can be controlled by herbicides and mowing (Zaremba 2001; Patten in press). Hybrid backcrossing into *S. foliosa* proceeds by positive feedback and accelerates without limitation, resulting in the local extirpation of *S. foliosa* where it grows with these hybrids (Ayres et al. 1999). Hybrid seed can be carried out of the Bay on tidal currents to colonize other estuaries and threaten *S. foliosa* beyond San Francisco Bay. Bolinas Lagoon, the estuaries on Point Reyes, and Tomales Bay are the closest to San Francisco Bay and probably most likely to be colonized. Stepping stone colonization and human aided movement may readily carry the hybrids to estuaries in southern and Baja California. For these reasons, we conclude that *S. foliosa* is in immediate danger of extirpation in San Francisco Bay, and perhaps beyond.

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NOTEWORTHY COLLECTIONS

ARIZONA

MAMMILLARIA THORNBERI Orcutt (CACTACEAE).—Pima County, locally fairly common beneath plants in sandy alluvium within a *Larrea divaricata-Atriplex* spp.-*Prosopis velutina*-mixed scrub Sonoran desertscrub association in northwestern Tucson, ca. 5.1 km E of Santa Cruz River and ca. 0.6 km S of Rillito Creek at a once rural residence just S of Tucson Mall along Wetmore Road near Neffson Drive, ca. 150–300 m E of Oracle Road, elevation 706 m, T13S, R13E, S24, NW¼ of SW¼, 32.286316N, −110.976779W, 11 August 2002, *R. Duncan s.n.* (ARIZ). The site, a 4.5 ha parcel, is the largest lot in the area that is currently not fully developed with extant Sonoran desertscrub; a single house, built in the middle of the 20th Century, currently exists on the site. Allan D. Zimmerman initially identified the Wetmore Road population and brought it to the attention of Gene Joseph, owner of Plants for the Southwest, Tucson.

Previous knowledge. Previously known from southwestern Arizona from as far north as just south of the Gila River near Komatke on the Gila River Indian Community, which is south of Phoenix, south through the Tohono O'odham Nation in western Pinal County and in Pima County, west of the Tucson Mountains to the southwest in Organ Pipe Cactus National Monument and south of the border into northwestern Sonora, Mexico where it is found as far south as southwest of Caborca (Benson 1969, The cacti of Arizona, University Arizona Press, Tucson, AZ; Paredes Aguilar, Van Devender and Felger, 2000, Cactáceas de Sonora, México: su diversidad, uso y conservación. Joint publication of IMADES, Hermosillo, Sonora, MX and Arizona-Sonora Desert Museum, Tucson, AZ). Within this range it is locally distributed in sandy alluvium of lower bajadas and valley bottoms. This cactus was formerly considered a federal candidate species for listing as threatened or endangered under the Endangered Species Act, however, it is no longer considered as such because it is not as rare as formerly believed.

Significance. First record in Tucson Basin E of Santa Cruz River and E of Tucson Mountains. Until this collection, the species had not been documented on the eastern side of the Tucson Mountains, which separates Avra Valley from the Tucson Basin of the Santa Cruz Valley (Benson 1969 and Rondeau et al. 1996, Desert Plants 12:1–46). The nearest known population of *M. thornberi* to this new record is ca. 22 km to the west in Avra Valley on the western side of the Tucson Mountains near the junction of Rudasill Road and Noel Lane at 32.31622N, −111.20423W (*R. Duncan s.n.,* ARIZ). It is expected that this remnant *M. thornberi* population E of the Santa Cruz River will be lost to development in the near future. It is surprising that it still remains (and has been overlooked for long), as the site is nearly surrounded by commercial and residential development, including being beside one of the largest shopping malls in Tucson. Additional surveys were conducted within 2 km of the Wetmore Road site and also between the site and the Santa Cruz River in areas where patches of similar desertscrub still remains at partially developed city parks and cemeteries, and also at older home sites in the area. Only a few additional plants were located at a nearby lot ca. 800 m SE of the Wetmore Road site at the SW corner of Limberlost Drive and Stone Avenue. This site is also scheduled for development.

—RUSSELL B. DUNCAN, Sage Landscape Architecture & Environmental, 2315 E. Speedway Blvd., Tucson, AZ 85719 (Current address: R. B. Duncan & Associates, 3315 N. Euclid Ave., Tucson, AZ. 85719. E-mail: rbduncan@theriver.com).

CALIFORNIA

LEGENERE LIMOSA (E. Greene) McVaugh (CAMPANULACEAE).—Santa Clara Co., Mt. Hamilton Range, Timber Ridge, Upper Twin Lake. UTM N 1,860,266.35 E 6,264,021.78, elev. approx. 610 meters. At edge of late ephemeral stock watering pond, under semi-shade of *Quercus lobata* Nee and around dried back pond margin within Ordinary High Water mark. Growing in areas of low vegetative cover and associated with *Lilaea scilloides* (Poiret) Hauman, *Rorippa curvisiliqua* (Hook) Britton, *Eleocharis macrostachya* Britton, and *Plagiobothrys* sp. Approximately 455 individuals, almost all in fruit. 11 June 2002. *Janell Hillman (voucher specimens submitted to JEPS and CAS).*

Previous knowledge. This rare plant is found in vernal pools and wet areas in California (J. C. Hickman [ed.] 1993, The Jepson Manual: Higher Plants of California, University of California Press, Berkeley) in Lake, Napa, Placer, Sacramento, Solano, San Mateo, Shasta, Sonoma, Tehama, and Yuba Counties (Corelli and Chandik 1995, The Rare and Endangered Plants of Santa Mateo and Santa Clara County, Monocot Press, Half Moon Bay; CNPS 2003, Inventory of Rare and Endangered Plants of California [6th edition, electronic version], Rare Plant Scientific Advisory Committee, D. P. Tibor, Convening Editor, California Native Plant Society, Sacramento). It is also documented for Alameda County, by Hannan et al. in 1999 (voucher in UC; Dieter Wilken, Santa Barbara Botanic Garden, pers comm. 2003). *Legenere* is endemic to California (CNPS 2001, Inventory of Rare and Endangered Plants of California [electronic version], Rare Plant Scientific Advisory Committee, D. P. Tibor, Convening Editor, California Native Plant Society, Sacramento).

Significance. This collection represents the first record of the taxon from Santa Clara County, and indicates a range extension and new southernmost distribution point.

—JANELL HILLMAN, Santa Clara Valley Water District, 5750 Almaden Expressway, San Jose, CA 95118. jhillman@valleywater.org.

MONTANA

ARABIS MURRAYI Mulligan (BRASSICACEAE).—Beaverhead Co., Pioneer Range, cirque N of Gorge Lake, uncommon in sandy soil on a gentle N-facing slope with *Phyllodoce empetriformis* and *Antennaria lanata,* 2865 m, T4S R11W S9. 14 Aug 1998, *Lesica 7748* (MONTU);

SW-facing slope of Comet Mtn., common in coarse-textured soil among boulders with *Tonestus lyallii* and *Aster alpigenus*, 3050 m, T4S R12W S26. 22 Jul 1991, *Lesica 5506* (MONTU). Determined by G. A. Mulligan (DAO).

Previous knowledge. Montana collections of this newly described species of the Canadian Rocky Mountains (Mulligan 1995, Rhodora 97:109–163) are 400 km S of the nearest station in southern Alberta.

Significance. First report for Montana and the U.S. Rocky Mountains.

CAREX GLACIALIS Mack. (CYPERACEAE).—Flathead Co., Flathead Range, 1.5 km E of the summit of Silvertip Mountain, common in a limestone fellfield on a windswept ridge with *Dryas octopetala* and *Carex rupestris*, 2500 m, T24N R13W S35. 31 Jul 2002, *Lesica 8522 with D. Hanna* (MONTU, ALA). Verified by D. Murray (ALA).

Previous knowledge. Our Montana collection of this arctic-subarctic sedge is 425 km SE of the closest disjunct station in Banff National Park, Alberta.

Significance. First collection for Montana and the continental U.S.

CAREX LENTICULARIS Michx. var. *DOLIA* (Jones) Standley (CYPERACEAE).—Park Co., Absaroka Mtns., NW side of Pine Creek Lake, uncommon in moist soil deposited among rock shelves with *Deschampsia cespitosa* and *Carex scirpoidea*, 2775 m, T4S R10E S14. 18 Aug 2000, *Lesica 8182* (MONTU, MICH). Verified by A. Reznicek (MICH).

Previous knowledge. 400 km SE of the Glacier National Park, previously the southernmost location for this taxon.

Significance. First report for the central Rocky Mountains.

FUMARIA VAILLANTII Lois. (FUMARIACEAE).—Fallon Co., ca. 22 km N of Baker; locally common in open soil on an E-facing slope of a green ash woodland with *Parietaria pennsylvanica* and *Carex sprengelii*. 990 m, T9N R60E S6. 4 Jun 2000, *Lesica 8062* (MONTU, GR). Verified by David Boufford (GH).

Previous knowledge. Introduced from Europe; in North America previously known only from E North Dakota and South Dakota; our collection is 300 km further west.

Significance. First report for Montana.

GITHOPSIS SPECULARIOIDES Nutt. (CAMPANULACEAE).—Sanders Co., Cabinet Range, W flank of Berray Mtn. 37 km SW of Libby; common in small patches at one site on a partially shaded granitic bedrock outcrop in a Douglas-fir-western larch forest with *Collinsia parviflora*, *Microsteris gracilis* and *Arenaria serpyllifolia*. 975 m, T27N R33W S4 SE¼. 12 Jun 1999, *Stickney 5666* (MRC, MONT, MNA); same location and date, *Lesica 7853* (MONTU). Duplicate of *Stickney 5666* verified by Nancy Morin (MNA).

Previous knowledge. 280 km NE of the nearest known location in SE WA (N. Morin personal communication).

Significance. First report for Montana.

PRIMULA ALCALINA Henderson & Cholewa (PRIMULACEAE).—Beaverhead Co., along Simpson Creek 1.5 km above the confluence with Cabin Creek; locally common in a wet alkaline meadow with *Juncus balticus* and *Deschampsia cespitosa*, 2150 m, T14S R11W S36. 26 Jun 2002, *Lesica 8450* (MONTU, COCO); along Cabin Creek 2 km above the confluence with Simpson Creek; common

on hummocks in a moist alkaline meadow with *Juncus balticus* and *Deschampsia cespitosa* 2165 m, T14S R11W S26. 8 Jul 2002, *Lesica 8500* (MONTU). *Lesica 8450* verified by Sylvia Kelso (COCO).

Previous knowledge. Known from several locations in E-central Idaho. Collected in adjacent Montana in 1936 (Rose 471, MONTU) but found to be extinct at that location.

Significance. The only known Montana population of this local endemic.

VULPIA BROMOIDES (L.) Gray (POACEAE).—Sanders Co., Cabinet Mtns., along Snake Creek Road 1.5 km S of Goat Rocks, locally common in sparsely vegetated, eroding soil below a rock outcrop with *Potentilla glandulosa* and *Lithophragma parviflorum*, 760 m, T27N R32W S5. 11 Jun 2000, *Lesica 8072 with P. Stickney* (MONTU, MONT). Duplicate verified by Matt Lavin (MONT).

Previous knowledge. Introduced from Europe; previously known from as far E as Idaho and Utah (Cronquist et al. 1977, Intermountain Flora).

Significance. First report for Montana.

—PETER LESICA, Herbarium, Division of Biological Sciences, University of Montana, Missoula, MT 59812; PETER STICKNEY, USDA Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807; DAVE HANNA, The Nature Conservancy, Pine Butte Swamp Preserve, HC 58 Box 34B, Choteau, MT 59422.

OREGON

CERASTIUM BRACHYPETALUM Pers. (CARYOPHYLLACEAE).—Benton Co., nw of Corvallis in the McDonald State Forest along Rd. 6021, flowers white, disturbed steep road bank with *Galium, Myosotis, Tonella, Nemophila, Senecio, Cirsium*, 44°37′36″N, 123°21′56″W, elev. 512 m, 27 May 2002, *R. Halse 6167* (OSC, MICH, duplicates to be distributed), identification verified by R. Rabeler.

Previous knowledge. This Eurasian species is found in eastern North America (H. Gleason & A. Cronquist, 1991, Manual of Vascular Plants of Northeastern United States and Adjacent Canada, 2nd ed.).

Significance. First report for OR.

JUNCUS COMPRESSUS Jacquin (JUNCACEAE).—Morrow Co., off of Interstate Hwy. 84 at Exit 151 (Threemile Canyon) ca. 19 km west of Boardman, on shores of the Columbia River with *Scirpus, Amorpha, Lepdium, Carex, Euthamnia*, 45°48′N, 119°57′W, elev. 76 m, 18 June 2001, *R. Halse 6017* (OSC, OSH); same place as above, 17 June 2002, *R. Halse 6194* (OSC, OSH, duplicates to be distributed), identification verified by N. Harriman.

Previous knowledge. This species is native to eastern North America and can be found as far west as MT and UT (R. Brooks & S. Clements, 2000, Juncaceae, In: Flora of North America 22:211–267).

Significance. First report for OR.

SCHOENOPLECTUS MUCRONATUS (L.) Palla [=*Scirpus mucronatus* L.] (CYPERACEAE).—Benton Co., E.E. Wilson Wildlife Area, 29555 Camp Adair Rd, ca. 11 km north of Corvallis, by canal west of Angling Pond, 44°42′23″N, 123°12′36″W, elev. 60 m, 18 Sept 1998, *D. Budeau*

(OSC); same place as above, wetlands with *Salix, Populus, Bidens, Carex, Sparganium, Typha,* 8 Oct 2000, *S. Stillwaggon* (OSC); same locality but in Killdeer Corner around edges of a pond constructed in 1995 with *Eleocharis, Alisma, Juncus, Bidens, Sparganium, Typha,* 44°43'09"N, 123°12'16"W, elev. 56 m, 14 Oct 2002, *R. Halse 6339* (OSC, duplicates to be distributed).

Previous knowledge. This Eurasian species is known from the eastern U.S. and CA; it is apparently cultivated, for wildlife food, but not established in Clark Co., WA (S. Smith, 2002, *Schoenoplectus.* In: Flora of North America 23:44–60).

Significance. First report for OR.

—RICHARD R. HALSE, Department of Botany and Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, OR 97331.

OREGON

ASTER BRACHYACTIS S. F. Blake (ASTERACEAE).— Morrow County: rest area on eastbound Interstate Highway I-84 west of Boardman; T4N R24E S14; UTM zone 11 285025e 5079043n. Elevation 100 m. Weed at edge of lawn in area of alkaline seeps in highly disturbed shrub steppe. Coll: Barbara L. Wilson 10876. Det: Scott Sundberg. 23 September 2002.

Previous knowledge. British Columbia to Minnesota, northern Washington to Wyoming and Missouri. (Hitchcock et al. 1955, Vascular Plants of the Pacific Northwest Part 5: Compositae, University of Washington Press, Seattle, WA).

Significance. First state record. Specimen deposited in the Oregon State University Herbarium (OSC).

CATALPA BIGNONIOIDES Walt. (BIGNONIACEAE).—Josephine County: Grants Pass, on Greenfield Road a few yards south of 6th Street. T36S R7W S5. Tree 2 m tall. One of about 8 small trees in the bottom of drainage ditch next to road, near a large planted ornamental tree. Flowers white with purple spots and lines and two yellow-orange bearded lines. Barbara L. Wilson 10968. 2 July 2003. MORROW COUNTY: Irrigon; east of intersection of 6th Street with Jane Avenue; UTM zone 11 319131e 508759n = 45°55.094'N 119°19.879'W. Elevation 60 m. Small tree growing on bank by bridge, between a hedge of *Populus nigra* and the highway. Barbara L. Wilson 10885. 7 October 2002. UMATILLA COUNTY: Hermiston; T4N R28E S10. Small tree in a fencerow between a store and a house. Long pods that are green or turning brown. This tree may have been planted, but saplings are coming up in a hedgerow. Other trees seen in fencerows and on roadsides, some in neglected areas where it is very doubtful they would have been planted. Barbara L. Wilson 10860. 23 September 2002.

Previous knowledge. Native in the southeast U.S. and naturalized in the northeast, to New England, the Great Plains, and Texas (Weedon, R. R., Bignoniaceae *in* Great Plains Flora Association, 1986, Fl. of the Great Plains, Univ. of Kansas Press, Lawrence, KS, p. 803). Planted as an ornamental, and saplings have been observed on roadsides at widely distributed sites in Oregon (pers. obs.).

Significance. First specimen documenting the existence of this naturalizing species in Oregon. Specimens deposited in the Oregon State University Herbarium (OSC).

COMMELINA COMMUNIS L. (COMMELINACEAE).— Umatilla County: Hermiston, on Highway 395; T4N R28E S10. Weed in ornamental shrub bed, with *Chamaesyce glyptosperma, Euphorbia serpyllifolia,* and *Oxalis corniculata.* Approximately three plants present, one larger and sprawling. Barbara L. Wilson 10856. 23 September 2002.

Previous knowledge. Native to east Asia, naturalized in the eastern U.S. west to the Great Plains and Texas (M. Bolick, *in* Great Plains Flora Association, 1986, Fl. of the Great Plains, Univ. of Kansas Press, Lawrence, KS, p. 1047).

Significance. First state record for Oregon. Specimen deposited in the Oregon State University Herbarium (OSC).

DATURA WRIGHTII Regel. (SOLANACEAE).—Gilliam County: Arlington; between China Creek and railroad tracks, within a block south of Highway 19. T3N R21E S28; UTM zone 10, 717595e 5066560n. Elevation 80 m. Foul-smelling bushy herbaceous plant, about 0.6 m tall, much branched. Flowers white, erect, but fruit nodding. Seeds tan (revisited in November; seeds still tan.) Growing in riprapped bank of stream, between stream and railroad tracks. Barbara L. Wilson 10852. 23 September 2002.

Previous knowledge. Native to Mexico, but occasional individuals found through much of California (Nee, 1993, *in* Hickman, ed., The Jepson Manual, University of California Press, Berkeley, CA, p. 1070) and the Great Plains (R. L. McGregor, J. L. Gentry, & R. E. Brooks, Solanaceae *in* Great Plains Flora Association, 1986, Fl. of the Great Plains, Univ. of Kansas Press, Lawrence, KS, p. 639). One previous Oregon record (G. Mason 13048, 30 Sept. 1975, Lane Co.: Eugene).

Significance. Second state record. Specimen deposited in the Oregon State University Herbarium (OSC).

LILAEOPSIS OCCIDENTALIS Coult. & Rose (APIACEAE).—Sherman County: Rufus; near end of road that runs west, between Interstate Highway I-84 and the Columbia River; T2N R16E S1 NE ¼. Elevation 75 m. Large rhizomatous patch in large gravel on east side of a small pond near the river. Associated species: *Salix* sp., *Coreopsis tinctoria* var. *atkinsoniana, Lycopus* sp. Barbara L. Wilson 10840. 13 September 2002. WASCO COUNTY: Celilo Village Park on the Columbia River; T2N R15E S20, UTM zone 10, approximately 658811e 5057164n. Elevation 60 m. Rhizomatous. Growing at shore of river, in fine-grained mud between small cobbles 7–15 cm in length, with *Sagina procumbens.* Barbara L. Wilson 10883. 28 September 2002.

Previous knowledge. This species is generally considered coastal (Hitchcock et al. 1961, Vascular Plants of the Pacific Northwest Part 3: Saxifragaceae to Ericaceae, University of Washington Press, Seattle, WA), though undocumented sightings have been made along the Columbia River (R. Halse pers. comm., K. Chambers pers. comm.).

Significance. These specimens document the occurrence of this species along the Columbia River east of the Cascade Range. Specimens deposited in the Oregon State University Herbarium (OSC).

PARTHENOCISSUS VITACEA (Knerr) Hitchc. (VITACEAE).—Gilliam County: Arlington; in marina between Interstate Highway I-84 and the Columbia River; T3N R21E S28; UTM zone 10, 717595e 5066560n. Elevation 80 m. Fruit dark blue, glaucous. Stem of inflorescence red. Vine scrambling over large rip-rap at edge of marina. As-

sociated species: *Amorpha fruticosa, Galium aparine, Cirsium arvense*. Barbara L. Wilson 10853. 23 September 2002. SHERMAN COUNTY: Rufus; T2N Rl7E S6 NE ¼. Elevation 75 m. Vine climbing on chain link fence by mowed lawn, with sapling *Morus alba* also growing in the fence. Barbara L. Wilson 10880. 28 September 2002. UMATILLA COUNTY: Hermiston; T4N R28E S10. Vine on chain-link fence. Berries dark blue, branches of infructescence bright red. This species moderately common on fences, hedgerows, and ornamental shrub beds around town and in anthropogenic habitats in nearby Washington. Any one plant (except the weeds in shrub beds) might be cultivated, but its frequency indicates the species is spreading on its own. Barbara L. Wilson 10842. 16 September 2002. WASCO COUNTY: The Dalles; north of Interstate Highway I-84; T1N R13E S1 and adjacent sections. UTM zone 10, approximately 642984e 5051248n.

Elevation 90 feet. Vine scrambling over ornamental junipers by trailer court, with *Cenchrus longispinus, Trifolium arvensis, Plantago lanceolata*. Barbara L. Wilson 10867. 23 September 2002.

Previous knowledge. Quebec to Manitoba & Montana, south to Wyoming & Texas (R. McGregor Vitaceae *in* Great Plains Flora Association, 1986, Fl. of the Great Plains, Univ. of Kansas Press, Lawrence, KS, p. 588). Scattered in towns and irrigated areas of south central Washington, growing on fences, shrubbery, and trees (pers. obs.). The few landowners questioned deny having planted it.

Significance. First specimen documenting the existence of this naturalizing species in Oregon. Specimens deposited in the Oregon State University Herbarium.

—BARBARA L. WILSON, Institute for Applied Ecology, 227 SW 6th Street, Corvallis, OR 97333.

MEMBERSHIP RENEWAL

Dear California Botanical Society Members,

We've made a big effort to get Madroño back on schedule, and we have finally reached our goal. You will receive Madroño 50(4) in January of 2004, and we will have two special issues of Madroño for 51(1) and 51(2). These two issues will be mailed together in early March 2004.

We normally send the first issue of each volume regardless of renewal status; however, this year we will not send any grace issues because of the combined mailing of the first two issues. **In order to ensure that you receive Madroño uninterrupted, you must renew your 2004 membership before January 28, 2004.** Check the date on your mailing label to see your current paid membership status. Because printing and mailing costs are substantial in producing Madroño, it is important for the Society to have an accurate count of membership before printing each volume of the journal. Your prompt membership renewal and support of the Society are greatly appreciated.

Renewal information (including rates and mailing information) can be found in the inside back cover of all Madroño issues and at the California Botanical Society web site (www.calbotsoc.org). In addition, renewal notices will be mailed to all current members in November 2003.

REVIEW

Aquatic and riparian weeds of the West. By JOSEPH M. DiTOMASO and EVELYN A. HEALY. 2003. University of California Agriculture and Natural Resources Publication 3421, 6701 San Pablo Avenue, Oakland, CA 94608-1239. 442 pp. Softcover $40.00 ISBN 1-879906-59-7.

This richly illustrated manual fills an open niche in our western botanical and weed science literature. And not only that—it is really enjoyable to use this book! Over 170 wetland species are described and illustrated by copious color photographs. Weedy species are often contrasted with non-weedy ones and, as a result, about a half of the included species are native. Identification keys are friendly, based on vegetative characters as far as possible. Characters of species in some larger and difficult genera (*Alisma, Sagittaria, Echinochloa, Phalaris, Polypogon, Polygonum, Potamogeton, Rumex, Scirpus, Spartina*) are summarized in tables that facilitate identification. Amateur botanists will appreciate the glossary of morphological terms. There is at least one photograph for 171 species. All the photographs are excellent, usually illustrating whole plants, their stands, and several important details, including seeds, achenes, spikelets, florets, stem cross-sections, etc. Joe DiTomaso and Jack Kelly Clark took almost all of them, mostly in the field. Evelyn Healy wrote most of the text and checked critical characters on hundreds of herbarium specimens. Finally, Ellen Dean, director of the Tucker Herbarium at UCD, assisted in the development of the keys. Portraits of all four contributors are on the last page of the manual and all of them deserve our congratulations.

I believe that this manual will serve a double purpose. Of course, weed scientists, weed science students, farm advisers, farmers, and managers of protected areas will use it for identification of wetland weeds. However, wetland biologists, who are primarily interested in ecology of aquatic, marsh, and riparian plants in California and surrounding states, will also use it as many common native wetland plants are included in the manual. Inevitably, however, some important native wetland genera are missing (we do not have any weedy species of *Carex* or *Downingia*)—this manual does not pretend to be replacement for Mason (1957). Several recently discovered invaders that are not covered by The Jepson Manual are included and illustrated (*Cabomba caroliniana, Limnobium laevigatum, Limnophila × ludoviciana, Salvinia molesta, Sesbania punicea*).

Only a very few western wetland weeds are missing in this book (e.g., *Agrostis stolonifera, Bidens* spp., *Conium maculatum, Distichlis spicata,* *Piptatherum miliaceum,* and *Rorippa nasturtium-aquaticum*). *Sapium sebiferum,* while still rare, would be worth a note (Bruce et al. 1997; Hrusa et al. 2002). Nomenclature is, in general, accurate and up-to-date. I can make only a few comments. *Eleocharis macrostachya* Britt. is not identical (p. 184) with *E. palustris* (L.) Roemer & Schultes (Smith et al. 2002). *Rubus armeniacus* Foke is not identical (=) with *R. discolor* Weihe & Nees (p. 348). *R. discolor* is a synonym for *R. ulmifolius* Schott (Weber 1995), another species mentioned in the text. Now, when also nominal variety of *R. ulmifolius* was discovered in California (Hrusa et al. 2002), absence of prickles on the stems (p. 352) remains a good character for var. *inermis* only. *R. ulmifolius* should be watched closely, as this is one of the worst weeds in Chile. As for *Tamarix,* the recent study by Gaskin and Schaal (2002) showed that the most common invasive plants in the U.S. are hybrids between *T. chinensis* and *T. ramosissima.* Common reed (*Phragmites australis*) is treated as a native species (p. 260). However, it is now known that an introduced invasive type is displacing native types in North America, including California (Saltonstall 2002).

The bibliography (pp. 412–424) provides some general references and references to specific genera. Several basic general references are missing (e.g., Casper and Krausch 1981; Flora of North America 2000, 2002; Galatowitsch et al. 1999; Grossinger et al. 1998; Guard 1995; Pieterse and Murphy 1990; Scultorpe 1967; Steward et al. 1960). References to specific genera are very unbalanced, seeming almost random: e.g., 11 references to *Elaeagnus,* only two references to *Cyperus,* one to *Salix,* no references to *Bacopa, Iris, Hydrocotyle,* or *Ludwigia.* Argus (1997), Barrett and Strother (1978), Sutherland (1990), Tucker et al. (2002), and Rejmánková (1992) provide useful information about the last six genera. There are three rather unspecific references under *Polygonum*; here, at least, Mitchell's (1968) monograph on *P. amphibium* (the species on the cover of the manual) should be listed. Ten references are listed under *Echinochloa*; however, the most recent one is from 1991. At least Asíns et al. (1999) and Fisher et al. (2000) could be mentioned. Some references to *Rubus* are under heading for *Rotala,* where probably Cook's (1979) monograph should be listed. There are whole books about *Eichhornia* that are ignored in the bibliography. Well, we could go on and on. But this is not what is important about this book!

This is an identification manual, written for a broad audience—from professional botanists to farmers, land mangers, and amateur botanists—all of whom will profit enormously from this book. I

have already learned a lot from it. This is one of those currently rare publications where the price per page is less than 10¢ and, even if it were somewhat more than that, it would be still worth the investment!

—MARCEL REJMÁNEK. Section of Evolution and Ecology, University of California, Davis, CA 95616.

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CALIFORNIA BOTANICAL SOCIETY
2003–2004 SCHEDULE OF SPEAKERS

All meetings are held at 7:30 p.m. on the 3rd Thursday of the month (except February)
Room 2063 Valley Life Sciences Building
University of California, Berkeley

September 18	Walter Koenig, Department of Integrative Biology, Hastings Reserve, University of California, Berkeley Ecology of acorn production by California oaks
October 16	Jeff Corbin, Department of Integrative Biology, University of California, Berkeley Native and exotic grasses in California: the view from coastal prairie grasslands
November 20	Gretchen LeBuhn, Department of Biology, San Francisco State University Evolution of competitive ability in wild mustard (*Brassica rapa*)
January 15	Michael Loik, Department of Environmental Studies, University of California, Santa Cruz Ecological responses to climate change in the western United States
February 15	**Annual banquet, Presidio Trust Log Cabin, San Francisco** **Harold Mooney, Department of Biological Sciences, Stanford University** **A personal view of California plant ecology: past, present and future**
March 18	Will Russell, Department of Biology, San Francisco State University and USGS/BRD/WERC, Golden Gate Field Station, Sausalito Conservation and restoration of coast redwood (*Sequoia sempervirens*) forests
April 15	Jean Langenheim, Department of Ecology and Evolutionary Biology, University of California, Santa Cruz What's so interesting about plant resins? More than you may now think!
May 20	Nishi Rajakaruna, Department of Biological Sciences, Stanford University Edaphic races in the *Lasthenia californica* complex: a case for parallel speciation

Seminars are open to all. Refreshments will be served following each seminar.
Information and reservation forms for the annual banquet will be mailed to Society members.

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CHROMOSOME COUNTS AND TAXONOMIC NOTES ON *DRABA* (BRASSICACEAE) OF THE INTERMOUNTAIN WEST. 2: IDAHO, NEVADA, AND VICINITY

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ABSTRACT

This paper presents a total of 28 chromosome counts for 16 different taxa of *Draba* (Brassicaceae) occurring in Idaho, Nevada, Oregon, and Utah. The chromosome numbers of *D. argyrea, D. arida, D. asterophora* var. *asterophora, D. burkei, D. cusickii, D. hitchcockii, D. jaegeri, D. lonchocarpa* var. *exigua, D. paucifructa, D. pedicellata, D. pennellii, D. sphaerocarpa,* and *D. sphaeroides* are reported here for the first time. The taxonomic significance of the new cytological data is discussed for each species. Based on the information now available, two new combinations are proposed: **Draba burkei** (C. L. Hitchc.) Windham & Beilstein comb. nov. and **Draba pedicellata** (Rollins & Price) Windham comb. nov. Counts of $n = 27$ appear to be the first reports of this number among the perennial drabas. In agreement with the previous paper in this series, species with aneuploid chromosome numbers predominate. Unlike the earlier data set, nearly half of the aneuploid taxa have chromosome counts greater than $n = 16$. Five of these appear to have originated through hybridization between the aneuploid and euploid lineages. These data indicate that reticulation between major clades, previously thought to be rare in *Draba,* may have played an important role in the evolution of the genus.

Key Words: aneuploid, chromosomes, *Draba,* Idaho, Intermountain West, Nevada, taxonomy.

This is the second in a planned series of papers reporting chromosome numbers for *Draba* (Brassicaceae) in the Intermountain West. The first paper (Windham 2000) focused on the flora of Utah, providing counts for a total of 11 *Draba* species including four of the seven taxa endemic to the state. In this second installment, I critically examine the drabas of Idaho, Nevada and adjacent areas. With a total of 12 endemics, these states support the greatest concentration of cytologically unknown species in the western United States. The goals of the study were: 1) to collect crucial chromosome data for local *Draba* species, 2) to critically assess current taxonomic treatments for the species sampled, and 3) to develop a set of chromosomally vouchered samples for ongoing DNA analyses of the genus.

MATERIALS AND METHODS

Chromosome counts were obtained and documented following the procedures outlined in the first paper of this series (Windham 2000). A full set of voucher specimens has been deposited at the Garrett Herbarium, Utah Museum of Natural History (UT). Additional duplicate vouchers have been sent to the herbaria listed in Table 1. To guide the discussion, I produced a compendium of published chromosome counts for all taxa studied and their putative relatives. This list was assembled by checking all accepted names and synonyms from Rollins (1993) and Kartesz (1999) in *Chromosome Numbers of Flowering Plants* (Federov 1974) and

a complete set of the Index to Plant Chromosome Numbers spanning the period 1965–1997 (Ornduff 1967, 1968; Moore 1973, 1974, 1977; Goldblatt 1981, 1984, 1985, 1988; Goldblatt and Johnson 1990, 1991, 1994, 1996, 2000). The primary literature was consulted to verify critical taxonomic and geographic information for counts identified by this search.

NOMENCLATURE

The following new combinations are made here.

Draba burkei (C. L. Hitchc.) Windham & Beilstein comb. and stat. nov. Basionym: *D. maguirei* C. L. Hitchc. var. *burkei* C. L. Hitchc.; Univ. Wash. Publ. Biol. 11: 72. 1941. Type: U.S.A., Utah, Box Elder Co., Wellsville Mountains, Cottonwood Canyon, southern exposure. Elev. 6300 ft. 25 May 1932. *M. Burke 2968* [Holotype: UTC!].

Draba pedicellata (Rollins & Price) Windham comb. and stat. nov. Basionym: *D. cusickii* B. L. Robins. ex O.E. Schulz var. *pedicellata* Rollins & Price; Harvard Papers Bot. 3: 73. 1991. Type: U.S.A., Nevada, White Pine Co., Cherry Creek Range, Pinenut Canyon, 2.2 road miles north of the Butte Valley road on the road to Last Chance Mine. T24N, R62E, S25. 8200 ft. 12 June 1987. *A. Tiehm 11242 & M. Williams* [Holotype: GH!]

RESULTS

My chromosome studies of *Draba* species occurring in Idaho, Nevada and adjacent areas yielded

TABLE 1. CHROMOSOME COUNTS ON *DRABA* FROM IDAHO, NEVADA AND VICINITY. Apparent first counts for a taxon are marked by a double asterisk following the relevant name. Latitude and longitude based on WGS84 Datum. Letters before collection numbers identify the following collectors: NH = Noel Holmgren; ER = Eric Rickart; FS = Frank Smith; JS = Joe Sirotnak; RS = R. Douglas Stone; W = Michael Windham; TW = Theresa Windham. Herbaria housing voucher specimens are identified by upper case abbreviations (Based on Holmgren et al. 1990) following the collection numbers.

Draba albertina Greene
n = 12	NV	White Pine Co.	along Baker Creek trail just SW of North Fork crossing in the Snake Range; *W, ER & JS 2175* (BRY, MO, NY, UT)
n = 12	UT	Duchesne Co.	NW slope of Blind Stream Peak in the Uinta Mts. (40°31′38″N 110°44′33″W); *W & TW 2199* (MO, UT)
n = 12	UT	Sanpete Co.	S side of John August Lake on the Wasatch Plateau (39°17′12″N 111°26′46″W); *W 2274* (ASU, BRY, COLO, CPH, MO, NY, UT, UTC)

Draba argyrea Rydb.**
n = 18	ID	Elmore Co.	WSW of Atlanta along James Creek (43°47′24″N 115°11′23″W); *W 2193* (ASU, BRY, MO, NY, UT)
n = 18	ID	Elmore Co.	W of Atlanta along Middle Fork of the Boise River (43°49′33″N 115°17′45″W); *W 2372* (COLO, CPH, UT, UTC, WTSU)

Draba arida C.L. Hitchc.**
n = 12	NV	Nye Co.	crest of the Toiyabe Range near head of Last Chance Creek (38°55′22″N 117°18′35″W); *W 2188* (ASU, MO, NY, UT)

Draba asterophora Payson** var. *asterophora*
n = 20	NV	Washoe Co.	NW of Carson City along NV 431 below Mt. Rose Summit (39°18′54″N 119°54′07″W); *W 2584* (ASU, COLO, MO, NY, UT)

Draba burkei (C.L. Hitchc.) Windham & Beilstein**
n = 10	UT	Box Elder Co.	in Cottonwood Canyon on W slope of the Wellsville Mts. (T10N, R2W, S2); *W, RS & FS 95-113* (ASU, BRY, COLO, DAO, MO, NY, UT)
n = 10	UT	Weber Co.	head of Upper Ogden Bowl on the N side of Mt. Ogden (T5N, R1E, S6); *W, NH & RS 95-168* (BRY, DAO, UC, UT, UTC)

Draba crassifolia Graham
n = 20	UT	Duchesne Co.	NW slope of Blind Stream Peak in the Uinta Mts. (40°31′38″N 110°44′33″W); *W & TW 2200* (MO, UT)
n = 20	UT	Piute Co.	S side of Bullion Canyon in the Tushar Mts. (T28S, R5W, S11); *W & RS 95-203* (UT)

Draba cusickii B.L. Robins. ex O.E. Schulz**
n = 13	OR	Harney Co.	SE of Frenchglen on Steens Mountain at head of Kiger Gorge (42°42′12″N 118°34′13″W); *W 2468* (ASU, COLO, MO, NY, UT)

Draba hitchcockii Rollins**
n = 27	ID	Butte Co.	ridge at mouth of Elbow Canyon in the Lost River Range (T7N, R26E, S18); *W 00-071* (ASU, COLO, CPH, MO, NY, UT)

Draba jaegeri Munz & Johnston**
n = 27, 2*n* = 54	NV	Clark Co.	along North Loop Trail at head of Deer Creek in the Spring Mts. (T19S, R57E, S18); *W 00-153* (ASU, COLO, MO, NY, UT)

Draba lonchocarpa Rydb. var *exigua* O.E. Schulz**
n = 8	UT	Summit Co.	S of Lonetree along East Fork of Beaver Creek near Hole in the Rock (40°56′38″N 110°09′49″W); *W 99-252* (UT)
n = 8	UT	Summit Co.	SW slope of Bald Mountain in the Uinta Mts. (T1S, R9E, S34); *W 95-215b* (MO, UT)

Draba oreibata J.F. Macbr. & Payson
n = 16	ID	Custer Co.	near head of Pass Creek Gorge in the Lost River Range (T7N, R25E, S2); *W 00-073* (ASU, COLO, CPH, MO, NY, UT)

Draba paucifructa Clokey & C.L. Hitchc.**
n = 20	NV	Clark Co.	NW of Las Vegas near base of Big Falls in the Spring Mts. (36°16′09″N 115°40′42″W); *W 2163* (MO, UT)

TABLE 1. CONTINUED.

Draba pedicellata (Rollins & Price) Windham**

n = 10	NV	Elko Co.	E of Wells along tributary of Maverick Canyon in the Pequop Range (41°03′51″N 114°35′51″W); *W 2054* (ASU, COLO, MON-TU, UT, UTC)
n = 10, 2n = 20	NV	Nye Co.	on ridge SE of Cherry Creek Summit in the Grant Range (T4N, R57E); *W 98-232* (COLO, ISTC, MO, NY, UT)
n = 10	NV	White Pine Co.	N of Cave Mountain along crest of the Schell Creek Range (39°11′10″N 114°36′44″W); *W 2181a* (MO, NY, UT)

Draba pennellii Rollins**

n = 16	NV	White Pine Co.	W side of Snake Range on knoll overlooking U.S. 50 (39°10′23″N 114°23′41″W); *W 2010* (ASU, MO, UT)
n = 16	NV	White Pine Co.	E of Ely above Steptoe Creek in the Schell Creek Range (39°13′40″N 114°40′33″W); *W 2047* (NY, UT, UTC)

Draba sphaerocarpa J.F. Macbr. & Payson**

n = 10	ID	Boise Co.	NE of Idaho City below campground on Edna Creek (43°57′21″N 115°36′28″W); *W 2370* (BRY, MO, UT)
n = 10	ID	Boise Co.	SE of Lowman along N Fork of the Boise River (43°54′13″N 115°26′25″W); *W 2371* (CPH, NY, UT, UTC)
n = 10	ID	Valley Co.	NE of Cascade along Trail Creek (44°37′39″N 115°44′58″W); *W 2064* (BRY, MO, NY, UT)

Draba sphaeroides Payson**

n = 10	NV	Elko Co.	upper Lamoille Canyon along Island Lake trail in the Ruby Mts. (40°36′35″N 115°22′32″W); *W 2191a* (ASU, COLO, UT); *W 2191b* (MO, NY, UT)
n = 10	NV	Elko Co.	along Jarbridge-Charleston road at Danger Point in the Jarbidge Mts. (41°48′46″N 115°28′25″W); *W 2459* (ASU, COLO, CPH, MO, NY, UT)

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a total of 28 counts for 16 different taxa (Table 1). Thirteen of these taxa have not been counted previously. These include *D. argyrea* Rydb. ($n = 18$), *D. arida* C. L. Hitchc. ($n = 12$), *D. asterophora* Payson var. *asterophora* ($n = 20$), *D. burkei* (C. L. Hitchc.) Windham & Beilstein ($n = 10$), *D. cusickii* B. L. Robins. ex O.E. Schulz ($n = 13$), *D. hitchcockii* Rollins ($n = 27$), *D. jaegeri* Munz & Johnston ($n = 27$), *D. lonchocarpa* Rydb. var. *exigua* O.E. Schulz ($n = 8$), *D. paucifructa* Clokey & C. L. Hitchc. ($n = 20$), *D. pedicellata* (Rollins & Price) Windham ($n = 10$), *D. pennellii* Rollins ($n = 16$), *D. sphaerocarpa* J. F. Macbr. & Payson ($n = 10$), and *D. sphaeroides* Payson ($n = 10$). Determinations of $n = 27$ appear to be the first reports of this number for the perennial drabas, extending the known series of aneuploid numbers in the group.

DISCUSSION

Draba albertina Greene

Based on detailed biosystematic studies of the *Draba crassifolia* complex in Canada, Mulligan (1975) resurrected the name *D. albertina* Greene for a taxon previously confused with *D. stenoloba* Ledeb. He noted that hybrids between these species were completely sterile, presumably due to differences in chromosome number ($n = 12$ in *D. albertina* vs. $n = 20$ in *D. stenoloba*). This taxonomy has not been widely accepted by botanists in the

Intermountain Region, and most recent floristic works from Utah (e.g., Arnow et al. 1980; Albee et al. 1988; Welsh 1993) continue to place *D. albertina* in synonymy under *D. stenoloba*. Reluctance to accept Mulligan's (1975) taxonomic treatment is founded, in part, on the limited size and geographic coverage of his sample (S. L. Welsh personal communication). His conclusions were based on a small number of chromosome counts (six for *D. albertina* and two for *D. stenoloba*), mostly from Canadian populations near the northern edge of the range. Windham (2000) provided the first counts for *D. albertina* from the Intermountain West, highlighting the occurrence of this species in Utah. With the addition of three more counts from Nevada and Utah (Table 1), the evidence is mounting that Mulligan's taxonomy applies equally well to populations in the southern portion of the range. All materials examined have the simple or once-forked adaxial trichomes characteristic of *D. albertina* and my chromosome counts of $n = 12$ confirm their assignment to this species.

Draba argyrea Rydb.

This is a rare species endemic to the mountains of central Idaho (Rollins 1993). Although yellow-flowered (often pale yellow), Hitchcock (1941) hypothesized that its closest relative was the white-flowered taxon *D. nivalis* Lilj. (=*D. lonchocarpa*).

Noting morphological similarities in a different direction, Rollins (1993) suggested that *D. argyrea* was related to *D. sphaerocarpa,* a yellow-flowered Idaho endemic that occurs at lower elevations in adjacent canyon systems. Cytological studies provide an unique opportunity to test these hypotheses because the proposed relatives have different chromosome base numbers. *Draba lonchocarpa* has been sampled rather extensively, with euploid counts of $n = 8$ or $2n = 16$ reported from Russia (Zhukova and Tikhonova 1971), Canada (Mulligan 1966, 1974), and now the United States (Table 1). Populations of *D. sphaerocarpa,* studied here for the first time, yielded aneuploid counts of $n = 10$ (Table 1). Rather than negating one hypothesis or the other, cytological studies of *D. argyrea* suggest that both are correct. The chromosome number of *D. argyrea,* determined in two different populations from Elmore County, Idaho, is $n = 18$ (Table 1). Given the shared morphological traits (Hitchcock 1941; Rollins 1993) and the additive chromosome number, it seems likely that *D. argyrea* is an allopolyploid derived through hybridization between *D. lonchocarpa* and *D. sphaerocarpa.*

Draba arida C. L. Hitchc.

This rare endemic is confined to the Monitor, Toiyabe and Toquima ranges of central Nevada (Rollins 1993). Its relationships rarely have been discussed, though Hitchcock (1941) indicated that it is most similar to members of the *D. ventosa* A. Gray complex. Studies of a population in the Toiyabe Range indicate that the chromosome number of *D. arida* is $n = 12$ (Table 1). This count suggests a close relationship to *D. ventosa* s.s., a taxon found in the Rocky Mountains from Utah to Alaska. Mulligan (1971) has shown that *D. ventosa* is an apomict with $2n = 36$. Although there are any number of ways to derive $2n = 36$ from lower numbers, Mulligan hypothesized that *D. ventosa* was a triploid based on $n = 12$. With the chromosome counts reported in this paper, only two members of Hitchcock's *ventosa* complex remain uncounted, the Californian species *D. cruciata* and *D. howellii.* Among the cytologically-known members of the complex, only *D. arida* shows $n = 12$. Considering the morphological affinities noted by Hitchcock (1941), it appears that *D. arida* is a relictual diploid that may have been involved in the polyploid origin of *D. ventosa* s.s.

Draba asterophora Payson

My data set includes a first count for *D. asterophora* var. *asterophora,* a rare endemic confined to the area around Mt. Rose, Nevada and the adjacent Sierra Nevada of California (Rollins 1993). Five plants from a relatively large population in Washoe County, Nevada yielded a chromosome number of $n = 20$ (Table 1). Although this number was clearly evident at anaphase I, multivalent chromosome associations hampered counts at earlier stages. Some cells at diakinesis showed ca. 10 quadrivalents, suggesting that they contained four sets of homologous chromosomes. Thus, my sample of var. *asterophora* appears to consist of tetraploids based on a chromosome number of $x = 10$. Neither var. *macrocarpa* nor *D. lemmonii,* the taxa considered most closely related by Hitchcock (1941), have been counted, so any discussion of relationships and polyploid origins would be premature.

Draba burkei (C. L. Hitchc.) Windham & Beilstein

The taxon herein called *D. burkei* (see Nomenclature section) previously has been treated as a variety (Rollins 1993) or a synonym (Welsh 1993) of *D. maguirei.* Both species are endemic to northern Utah, with *D. burkei* occurring in the Wasatch and Wellsville Mountains and *D. maguirei* confined to the Bear River Range. Although found in the same general region, the two taxa are allopatric, with the closest known populations separated by 11 km. This geographic disjunction coincides with differences in trichome type that prompted Rollins (1993: 432) to comment that "variety *burkei* may deserve specific rank". The first chromosome counts reported here for *D. burkei* support the idea that it should be treated as a distinct species. Two samples of *D. burkei,* representing the southern (Wasatch) and northern (Wellsville) populations, yielded counts of $n = 10$ (Table 1). *Draba maguirei* var. *maguirei,* on the other hand, has been reported previously as $n = 16$ (Windham 2000). The divergent chromosome numbers of the two taxa suggest that they are not closely related, a fact confirmed by recent DNA studies (Windham and Beilstein unpublished).

Draba crassifolia Graham

This taxon has been included in several previous cytological studies. Counts of $n = 20$ or $2n = 40$ have been reported from Norway (Engelskjøn and Knaben 1971; Brochmann et al. 1992a), Greenland (Heilborn 1941; Dalgaard 1989), Canada (Mulligan 1966, 1975), and now the United States (Table 1). The only two reports deviating from this number, both found in the *Index to Plant Chromosome Numbers,* can be dismissed as erroneous. A count of $n = 40$ published by Ornduff (1968) and attributed to Mulligan (1966) is nowhere to be found in Mulligan's paper and clearly represents a mistranscription of a $2n = 40$. The report of $2n = 64$ published by Goldblatt and Johnson (1996) also is unfounded. The Brochmann (1993) paper cited as the original source contains no new counts, stating that all cytological data derive from Brochmann et al. (1992a), which lists just two counts ($n = $ ca. 20 and $2n = 40$) for *D. crassifolia.*

Despite general agreement on the chromosome number of *Draba crassifolia,* widely divergent

opinions exist regarding the ploidy level and origin of this number. The species has been cited as a pentaploid based on $x = 8$ (Koch and Al-Shehbaz 2002), an octoploid based on $x = 5$ (Brochmann 1993) and a tetraploid based on $x = 10$ (Mulligan 1975). The idea that *D. crassifolia* is pentaploid reflects the assumption that *Draba,* the largest genus of the Brassicaceae, has a single chromosome base number ($x = 8$). There is ample evidence to the contrary, especially in North America where the species exhibit a complete series of aneuploid base numbers between $n = 8$ and $n = 16$ (Mulligan 1976; Windham 2000). Recent DNA studies by Beilstein and Windham (2003) indicate that North American aneuploids form a well-supported clade distinct from the $x = 8$ euploids. These analyses also confirm that *D. crassifolia* is a core member of this aneuploid lineage (Beilstein and Windham 2003, Figs. 1 and 2). None of the species belonging to this clade has a chromosome number based on $x = 8$, and there is no reason to consider *D. crassifolia* an exception. This is especially true considering that a base number of $x = 8$ would make the taxon pentaploid, which is incongruent with the fact that *D. crassifolia* is sexually reproductive and fully fertile (Mulligan 1975).

The number of duplicated isozyme loci observed in *Draba crassifolia* led Brochmann (1993) to consider this taxon an octoploid based on $x = 5$. However, there are other ways to account for these duplications without invoking an unusually low base number that has not been found in any species of *Draba.* In fact, all members of the North American aneuploid lineage examined to this point show extra isozyme loci (Windham unpublished), suggesting that the processes of aneuploid evolution and enzyme duplication are somehow linked in this group. Given the extensive duplication observed in species of this clade, Mulligan's (1975) hypothesis that *D. crassifolia* is a tetraploid based on $x = 10$ is quite sufficient to explain the number of loci observed by Brochmann (1993). And, unlike the elusive $n = 5$ progenitor, species with $n = 10$ are common in the aneuploid lineage (Table 1).

Although Mulligan's hypothesis is the most parsimonious explanation offered to date, none of the extant species of *Draba* with $n = 10$ provide likely parents for the tetraploid. It is possible that populations of *D. crassifolia* showing $n = 20$ represent autotetraploids derived from a morphologically cryptic diploid ($n = 10$). However, strict formation of bivalents during meiosis argues against this scenario, especially in light of the pairing behavior observed in plants of *D. asterophora* var. *asterophora* with $n = 20$ (see earlier discussion). Based on the chromosome data now available, I suggest a modification of Mulligan's (1975) hypothesis for the origin of *D. crassifolia.* Rather than being a tetraploid based on $x = 10$, I propose that *D. crassifolia* is a heterobasic tetraploid resulting from hybridization

between *D. albertina* ($n = 12$) and a white-flowered euploid ($n = 8$) resembling *D. fladnizensis* Wulfen.

Several lines of evidence support this heterobasic tetraploid hypothesis. *Draba crassifolia* is intermediate between the proposed parental species in most of the characters examined (Table 2). It is considered "very closely related" (Mulligan 1975: 751) to *D. albertina,* so much so that the two species often are confused (Hitchcock 1941; Welsh 1993). A close relationship to *D. fladnizensis* is supported by Rollins' comment that "If flower color is not known, some specimens . . . are difficult to distinguish from *D. crassifolia.*" (Rollins 1993: 414). Hybridization between *D. albertina* and *D. fladnizensis* would explain most of the features of *D. crassifolia* that set it apart from other members of the aneuploid lineage, including the sparse, usually simple pubescence, the pale yellow to cream-colored flowers and the unusual chromosome number (Table 2). It also would account for chromosome configurations observed in artificial hybrids between *D. crassifolia* and *D. albertina,* where some cells showed approximately 12 bivalents and 8 univalents at metaphase I (Mulligan 1975). This is the kind of chromosome pairing behavior expected in a backcross between a tetraploid and one of its diploid progenitors. Based on the heterobasic tetraploid hypothesis, I suggest that the genome of *D. albertina* ($n = 12$) is pairing with the homologous chromosome set present in *D. crassifolia,* leaving the eight chromosomes derived from *D. fladnizensis* unpaired. If this interpretation proves correct, *D. crassifolia* would join a rapidly expanding list of species originating through hybridization between the euploid and aneuploid lineages of *Draba* (see discussion below).

Draba cusickii B. L. Robins. ex O. E. Schulz

In its typical form, *D. cusickii* is endemic to Steens Mountain in southeastern Oregon (Rollins 1993). I visited this area during the 2001 field season and obtained chromosome counts of $n = 13$ (Table 1) from a population at the head of Kiger Gorge. Hitchcock (1941) treated *D. cusickii* as a variety of *D. sphaeroides,* whereas Rollins (1993) considered it a separate species with two varieties, var. *cusickii* and var. *pedicellata* Rollins & Price. Counts of all three taxa are reported here for the first time, allowing a cytological assessment of previous classifications. Both *D. sphaeroides* and *D. cusickii* var. *pedicellata* [herein called *D. pedicellata* (Rollins & Price) Windham; see discussion below] show chromosome numbers of $n = 10$ (Table 1). This discovery prompted a reevaluation of morphological differences among the taxa (Table 3), culminating in the conclusion that *D. cusickii* is quite distinct from both of its former associates. For this reason, *D. cusickii* is treated here as a discrete species without varieties. Beyond the kinship implied by earlier taxonomic treatments, the only oth-

TABLE 2. COMPARISON OF SELECTED TAXA OF INTERMOUNTAIN *DRABA* DEMONSTRATING POSSIBLE HYBRID ORIGINS OF *D. PAUCIFRUCTA* AND *D. CRASSIFOLIA*. Adapted from Hitchcock (1941: 106) with additional information from Arnow et al. (1980), Mulligan (1974, 1975), Rollins (1993), and Welsh (1993).

Characters/Taxa	*D. lonchocarpa*	*D. paucifructa*	*D. albertina*	*D. crassifolia*	*D. fladnizensis*
Habit	Perennial; caudex usually branched	Perennial; caudex simple or branched	Weakly perennial to biennial; caudex usually simple	Weakly perennial; caudex usually simple	Perennial; caudex simple or branched
Leaf length	to 15 mm	to 25 mm	to 35 mm	to 30 mm	to 25 mm
Trichomes on abaxial leaf surfaces	Mostly dendritic with 8+ rays	Mostly branched with 4 to 7 rays	Mostly branched with 2 to 4 rays	Simple to 2-rayed (rarely absent)	Simple or absent
Trichomes on lower stems	Dendritic	Mostly branched with 2 to 3 rays	Simple or bifid	Absent (or simple)	Absent (or simple)
Cauline leaves	0 (rarely 1)	0 to 2	1 to 3 (rarely 4)	0 (rarely 1 to 2)	0 (rarely 1 to 2)
Petal color	White	Pale yellow in bud, white at anthesis	Yellow at anthesis (rarely pumpkin)	Yellow (usually pale) to cream	White
Style length	0.2 to 0.5 mm	0.1 to 0.3 mm	0.05 to 0.1 mm	0.05 to 0.1 mm	0.05 to 0.1 mm
Chromosome #	$n = 8$	$n = 20$	$n = 12$	$n = 20$	$n = 8$

er clue to relationships comes from Rollins' comment that "*Draba sobolifera* is related to *D. cusickii*" (Rollins 1993: 453). This is an intriguing statement in light of the fact that *D. sobolifera,* a southern Utah endemic, is one of only two species of *Draba* previously shown to have a chromosome number of $n = 13$ (Windham 2000). Thus, the cytological data reinforce morphological evidence that *D. cusickii* and *D. sobolifera* are closely related, despite their substantial geographic isolation.

Draba hitchcockii Rollins

Only recently discovered due to its rarity, this species is endemic to the area around the Lost River Range in east central Idaho (Rollins 1983). Six plants from a population near the type locality in Elbow Canyon yielded chromosome counts of $n = 27$ (Table 1), apparently the first report of this number for the perennial drabas. In comments accompanying the original description, Rollins (1983: 501) stated that "although *D. hitchcockii* has white flowers, it is undoubtedly most closely related to the yellow-flowered *D. paysonii* Macbr. var. *paysonii. . . .*" Chromosome counts have not been published for var. *paysonii,* though var. *treleasii* (O.E. Schulz) C.L. Hitchc., which Rollins (1983) considers more distantly related, shows $2n = 42$ (Mulligan 1971). Neither the flower color of *D. paysonii* nor the chromosome number of var. *treleasii* seem to suggest an especially close relationship to *D. hitchcockii.*

Draba jaegeri Munz & Johnston

The true phylogenetic affinities of *D. hitchcockii* might have remained a mystery if not for the serendipitous addition of *D. jaegeri* to this study, and the inclusion of both species in a recent DNA analysis by Koch and Al-Shehbaz (2002). *Draba jaegeri* is a rare endemic of the Spring (Charleston) Mountains in southern Nevada, located nearly 875 km distant from the range of *D. hitchcockii.* Hitchcock, who was unaware of the species ultimately named for him, considered *D. jaegeri* "about the most distinct of our western Drabas." (Hitchcock 1941: 54). I first encountered *D. jaegeri* a few weeks after collecting *D. hitchcockii,* and was immediately struck by the morphological similarities between them. Caespitose drabas with large, white flowers are rare in the Intermountain West, and the two species look very similar in the field. Chromosome counts confirmed my initial suspicion that these geographically isolated taxa were somehow related. Five plants of *D. jaegeri,* collected a few kilometers NE of the type locality, exhibited a chromosome number of $n = 27$, $2n = 54$ (Table 1). *Draba jaegeri* is only the second perennial species to show this number, the other, of course, being *D. hitchcockii.*

The relatively high, aneuploid chromosome number of these species suggests that they originated

TABLE 3. Morphological and Chromosomal Comparison of *Draba cusickii*, *D. pedicellata* and *D. sphaeroides.* Data from published sources (Hitchcock 1941; Price and Rollins 1991; Rollins 1993) and herbarium specimens at UT.

Characters/Taxa	*D. cusickii*	*D. pedicellata*	*D. sphaeroides*
Habit	Loosely caespitose; caudex branches few, discrete, to 3 cm long	Loosely caespitose; caudex branches few, discrete, to 5 cm long	Mat-forming; caudex branches numerous, tangled, to 10 cm long
Leaf shape	Obovate to broadly oblanceolate	Oblanceolate or (rarely) obovate	Elliptic to narrowly oblanceolate
Leaf length	to 12 mm	to 15 mm	to 9 mm
Leaf surface trichomes	Predominantly cruciform (a few 2- to 3-rayed)	Mixed cruciform, 2- to 3-rayed and (rarely) simple	Mixed cruciform, 2- to 3-rayed and (rarely) simple
Leaf definition	Largest leaves obscurely toothed	All leaves entire	All leaves entire
Simple cilia near leaf base	Very rare	Very rare	Often present
Lower stem pubescence	Abundant; dendritic to cruciform (rarely some simple); to 0.6 mm long	Variable; mostly 2- to 3-rayed (rarely some simple); to 1.2 mm long	Sparse; 2- to 3-rayed (rarely some simple); to 0.6 mm long
Upper stems and pedicels	Pubescent like lower stems	Nearly glabrous	Glabrous or (rarely) like lower stem
Pedicel base	Neither expanded nor decurrent; ca. half as wide as the rachis above	Expanded & somewhat decurrent; often nearly as wide as the rachis above	Expanded & somewhat decurrent; often nearly as wide as the rachis above
Pedicel orientation	Ascending; ± straight	Widely spreading; straight or curved upward	Spreading-ascending; curved upward or straight
Infructescences	Elongate, at least 3× longer than wide	Subcorymbose to elliptic, often less than 2× longer than wide	Elliptic to elongate, at least 2× longer than wide
Fruit pubescence	Abundant; cruciform	Absent or sparse to (rarely) abundant; 2-rayed or simple	Absent or sparse; 2- to 4-rayed or simple
Fruit length	to 9 mm	to 13 mm	to 8 mm
Fruit width	to 5 mm	to 5.5 mm	to 3 mm
Chromosome #	*n* = 13	*n* = 10	*n* = 10

through hybridization and polyploidization. This idea is supported by the DNA analyses of Koch and Al-Shehbaz (2002). They found that *D. hitchcockii* and *D. jaegeri* shared a unique combination of characters in the ITS region, which they hypothesized resulted from gene exchange between two major lineages (Clades IV and VI in their analysis). I suggest that both species were produced by hybridization between a white-flowered euploid species with *n* = 16 and a yellow-flowered aneuploid with *n* = 11. Whether they are descended from a single common ancestor or were produced by independent hybridization events remains to be seen, but the available data (including the DNA sequences) seem to favor independent hybridization. Based on morphology and geography, I suspect that *D. pennellii* (counted here for the first time; see Table 1) is the euploid parent of *D. jaegeri* whereas *D. oreibata* is the euploid parent of *D. hitchcockii.* Considering the number of presumed aneuploids that remain uncounted, the specific source of the aneuploid genomes is less certain. The aneuploid parent of *D. jaegeri* might be *D. kassii* Welsh, which has a chromosome number of *n* = 11 and grows less than 70 km from the putative euploid parent *D. pennellii.* Although *D. paysonii* var. *paysonii* has yet to be counted, the morphological similarities between it and *D. hitchcockii* (see Rollins 1983) suggest that it is a good candidate for the aneuploid parent of that species.

Draba lonchocarpa Rydb.

This species is widespread in western North America, extending from California and Colorado to Alaska, and is found in eastern Asia as well. It is very similar to *D. nivalis* (see Arnow et al. 1980) and was included in that largely boreal species by Hitchcock (1941). Despite the similarity of these taxa, Mulligan (1974) reported that artificial hybrids were completely sterile, and he treated *D. lonchocarpa* and *D. nivalis* as separate species. Mulligan (1974) and Rollins (1993) further subdivide *D. lonchocarpa* into three varieties: var. *lonchocarpa*, var. *thompsonii* (C. L. Hitchc.) Rollins, and var. *vestita* O.E. Schulz. Welsh (1993) recognized an additional infraspecific taxon (var. *exigua*) that was placed in synonymy under var. *lonchocarpa* by the other authors. Although var. *exigua* and var. *lonchocarpa* appear as sister taxa in the DNA analysis of Beilstein and Windham (2003), their ITS sequences are more divergent than those of some unquestioned species (e.g., *D. sobolifera* and *D. sub-*

alpina). As such, it seems wise to maintain var. *exigua* as a distinct taxon pending further study.

Previous cytological work on *Draba lonchocarpa* has shown it to be uniformly diploid with chromosome numbers of $n = 8$ or $2n = 16$. The typical variety has been counted from several regions, including the Chukhotsk Peninsula of Russia (Zhukova and Tikhonova 1971) and the mountainous provinces of western Canada (Mulligan 1966, 1974). Variety *thompsonii*, which Rollins (1993) considers endemic to the Cascade Mountains of western Washington, apparently has not been studied cytologically. The chromosome number of var. *vestita* is known from a single population on the Queen Charlotte Islands of British Columbia (Mulligan 1974). New counts reported here appear to be the first for var. *exigua* and the first for *D. lonchocarpa* from the United States. Two populations from the Uinta Mountains of northeastern Utah yielded counts of $n = 8$ (Table 1) and thus are in agreement with previous counts for the species.

Draba oreibata J. F. Macbr. & Payson

Recent taxonomic treatments of this species (i.e., Tiehm and Holmgren 1991; Rollins 1993) recognize two varieties: var. *oreibata* and var. *serpentina* Tiehm & P. Holmgren. The type variety apparently is endemic to the mountains of east central Idaho, though there are unconfirmed reports from adjacent areas of Montana (Rollins 1993). Located more than 600 km to the southwest, var. *serpentina* is a Nevada endemic currently known from the Snake and Toiyabe Ranges (Tiehm and Holmgren 1991). Although the two taxa look quite similar, they have different chromosome base numbers (Windham & Allphin unpublished) and there is growing evidence that var. *serpentina* is an allopolyploid. In anticipation of an upcoming paper (Windham & Allphin in preparation) that will raise var. *serpentina* to species status, the name *D. oreibata* is here restricted to the typical plants of eastern Idaho and vicinity. This taxon has been counted previously (Henderson et al. 1980) from Custer County, Idaho, and my determination of $n = 16$ (Table 1) from the same area corroborates the original report. The count confirms that *D. oreibata* is a member of the white-flowered euploid lineage that may be related to *D. alpina* (see Hitchcock 1941). A purported close relationship to *D. subalpina* Goodman & C. L. Hitchc. (Hitchcock 1941) is not supported by chromosome or DNA data. *Draba subalpina*, a southern Utah endemic with $n = 13$, is a core member of the aneuploid clade (Beilstein and Windham 2003) with ITS sequences identical to *D. sobolifera* (also $n = 13$). Thus, the white flowers of *D. subalpina* are not indicative of a relationship to *D. oreibata*; they are, in fact, the product of an autapomorphic reversal of flower color within the aneuploid lineage (see Beilstein and Windham 2003: Fig. 1).

Draba paucifructa Clokey & C. L. Hitchc.

This taxon is a rare endemic of the Spring (Charleston) Mountains in southern Nevada. The species combines traits associated with different lineages in *Draba*, and its relationships have been characterized as "exceedingly perplexing" (Hitchcock 1939: 128). In comments accompanying the original description, Hitchcock stated that ". . . it might feasibly be accorded varietal rank under *D. nivalis* Lilj. (*D. lonchocarpa* Rydb.). However, it cannot with certainty be considered more closely related to that species than to *D. crassifolia* Grah. or even to *D. stenoloba* Ledeb." (Hitchcock 1939: 128–129). In other words, *D. paucifructa*, like *D. crassifolia*, is more or less intermediate between members of the white-flowered euploid clade (*D. lonchocarpa* and its allies) and the yellow-flowered *D. albertina* (considered a var. of *D. stenoloba* by Hitchcock (1941)). This can be seen in a variety of morphological characters, including habit, trichome types and style length (Table 2). Even the unusual flower color of *D. paucifructa* is intermediate, with the petals appearing light yellow when the buds first open and immediately fading to white. Given the clear evidence of morphological intermediacy, it is not surprising that the chromosome number is additive as well (Table 2). Two plants of *D. paucifructa*, collected within 3 km of the type locality, yielded counts of $n = 20$ (Table 1). This number is shared with *D. crassifolia*, and it might be argued that *D. paucifructa* is simply an isolated, southern derivative of that species. However, the morphological data seem to favor independent origins (Table 2), and I am convinced that *D. paucifructa* arose through hybridization between *D. lonchocarpa* and *D. albertina*.

Draba pedicellata (Rollins & Price) Windham

The taxon herein called *D. pedicellata* (see Nomenclature section) previously has been treated as a variety of *D. cusickii* (Price and Rollins 1991; Rollins 1993) or subsumed under *D. sphaeroides* var. *sphaeroides* (Hitchcock 1941). Table 3 lists all of the characters that have been used to distinguish the three taxa. In habit, leaf shape, fruit width, and the near absence of simple cilia on the leaves, *D. pedicellata* is most similar to *D. cusickii*. Fruit length has been cited as an additional feature by these taxa (Price and Rollins 1991), but new data for *D. sphaeroides* close the gap between it and *D. cusickii*. Thus, *D. pedicellata* shows the highest values for fruit length, as it does in most other quantitative characters (Table 3).

In the paper naming *Draba cusickii* var. *pedicellata*, Price and Rollins (1991) mentioned two features separating it from the typical variety: qualitative differences in fruit pubescence and the absence of trichomes on the upper stem and inflorescence. As noted by Hitchcock (1941), both of these characters suggest a relationship to *D. sphaeroides*.

In fact, the list of features distinguishing *D. pedicellata* from *D. cusickii* and linking the former to *D. sphaeroides* is substantially longer (Table 3). Among the morphological traits supporting a relationship to *D. sphaeroides* are leaf surface trichomes, leaf dentition, pedicel orientation, and the unusual pedicel bases. The latter features probably inspired the epithet *pedicellata,* the etymology of which was never explained. A subtle combination of pedicel orientation, curvature, and attachment produce a rather distinctive form of inflorescence (often resembling a candelabra) that is characteristic of both *D. pedicellata* and *D. sphaeroides.* In two other characters, lower stem pubescence and shape of the infructescences, *D. pedicellata* is most similar to *D. sphaeroides* but exhibits more extreme quantitative values (Table 3).

Based on overall morphological similarity and the types of traits involved, I would tend to agree with Hitchcock (1941) that the populations herein assigned to *D. pedicellata* are more closely related to *D. sphaeroides* than they are to *D. cusickii.* Other authors (e.g., Price and Rollins 1991; Rollins 1993) emphasize a different subset of the characters in Table 3 and come to different conclusions. Without knowing which characters truly reflect phylogeny, we must turn to other techniques to supplement the data set. Because the proposed relatives have different chromosome base numbers ($n = 13$ in *D. cusickii* and $n = 10$ in *D. sphaeroides*), cytological information on *D. pedicellata* can provide additional insight into the question of relationship. I sampled three populations of *D. pedicellata,* representing most of the latitudinal and altitudinal range of the species. All collections yielded counts of $n = 10$ or $2n = 20$ (Table 1). The chromosome data thus combine with the majority of morphological traits to support Hitchcock's (1941) hypothesis that *D. sphaeroides,* not *D. cusickii,* is the closest relative of *D. pedicellata.* In light of these data, I am convinced that *D. pedicellata* should not be maintained as a variety of *D. cusickii.* Although subsuming it under *D. sphaeroides* (its putative sister taxon) would be an option, the two taxa are amply distinct (Table 3). Both are endemic to eastern Nevada, but they occupy different mountain ranges and show no signs of intergradation. Therefore, I treat *D. pedicellata* as a separate species with probable relationships to other $n = 10$ taxa such as *D. sphaeroides* and *D. sphaerocarpa.*

Draba pennellii Rollins

Like *D. hitchcockii,* this is a rare species that was not described until 1983; it is known only from the mountains of eastern Nevada (Rollins 1993). Two chromosome samples of *D. pennellii,* representing the eastern (Snake Range) and western (Schell Creek Range) populations, yielded counts of $n = 16$ (Table 1). In comments accompanying the original description, Rollins (1983: 503) stated that

"The habit of growth is much like *D. sphaeroides,* and I am inclined to associate *D. pennellii* with that species." However, the highly branched, loosely matted, fragile caudices shared by these taxa are found in distantly related taxa worldwide and, in some species, can be environmentally induced. Rollins (1983) went on to list an impressive array of features that distinguish *D. pennellii* from *D. sphaeroides,* including leafy fertile stems, white flowers, obovate petals sharply differentiated into blade and claw, and dense pubescence extending up the fertile stems to include the pedicels. To this list, we now may add chromosome number, which is $n = 16$ in *D. pennellii* and (reported here for the first time) $n = 10$ in *D. sphaeroides* (Table 1). Given the flower color, chromosome number, and other characteristics of *D. pennellii,* it is unlikely to be related to *D. sphaeroides.* Its close relatives should be sought among such white-flowered euploids as *D. oreibata* and *D. smithii* Gilg. ex O.E. Schulz.

Draba sphaerocarpa J. F. Macbr. & Payson

This is an Idaho endemic restricted to canyons and lower slopes of the mountains north and east of Boise. Three populations from Boise and Valley counties yielded chromosome counts of $n = 10$ (Table 1). The species has been considered a close relative of *D. argyrea* by every author who studied it (Payson 1917; Hitchcock 1941; Rollins 1993), and Schulz (1927) treated it as a variety of that species. My chromosome data suggest a reason for this association; it appears that *D. sphaerocarpa* ($n = 10$) may have hybridized with *D. lonchocarpa* ($n = 8$) to produce the heterobasic tetraploid *D. argyrea* (see earlier discussion). Some of the intermediate specimens and seed sterility discussed by Hitchcock (1941) may be due to backcrossing between *D. argyrea* and *D. sphaerocarpa* in the Sawtooth Mountains where their ranges overlap. Beyond *D. argyrea,* the relationships of *D. sphaerocarpa* probably lie with other $n = 10$ species such as *D. pedicellata* and *D. sphaeroides.*

Draba sphaeroides Payson

Although this species is endemic to the mountains of northeastern Nevada, it shows considerable morphological variation (Rollins 1993). Chromosome materials were gathered from three different morphotypes to ascertain whether this variability was reflected in the cytology of the plants. One sample came from a relatively invariant, northern population situated ca. 8 km from the type locality in the Jarbidge Mountains. Two additional collections represent morphological extremes within a variable population in the Ruby Mountains, located near the southern edge of the species range. All samples yielded counts of $n = 10$ (Table 1), congruent with field observations that the variants intergrade freely. *Draba sphaeroides* probably is most closely related to *D. pedicellata* (see earlier

discussion), which has the same chromosome number, occurs in adjacent mountain ranges, and was included in *D. sphaeroides* var. *sphaeroides* by Hitchcock (1941). The relationship to *D. cusickii* probably is not as close as Hitchcock (1941) hypothesized. The taxa are quite distinct (Table 3), and many of the morphological similarities noted by Hitchcock likely represent pleisiomorphic traits within the aneuploid lineage. In light of recent DNA studies (Beilstein and Windham 2003), the divergent chromosome base numbers of *D. sphaeroides* and *D. cusickii* suggest that they are not sister taxa.

CONCLUSIONS

With the chromosome counts reported above, Idaho and Nevada no longer are *terra incognita* so far as the cytology of *Draba* is concerned. They have, instead, become one of the best sampled regions of the United States. Ten of the twelve taxa confined to this area now have been analyzed chromosomally. As in the adjacent state of Utah (Windham 2000), species with aneuploid chromosome counts greatly outnumber those with euploid base numbers. This confirms the suggestion made in the previous paper that the Intermountain West is a primary center of diversity for aneuploid *Draba*. Among the aneuploids in this region, counts of $n = 10$ appear to predominate but taxa with $n = 12$ also are relatively common. Counts of $n = 13$ remain rare; the Oregon endemic *Draba cusickii* is only the third species worldwide to exhibit this number. Although a complete series of aneuploid base numbers extending from 8 to 16 has been reported by other studies (Mulligan 1976; Windham 2000), species with $n = 9, 11, 14$ and 15 are not represented in the current sample.

In sharp contrast to the earlier paper in this series (Windham 2000), nearly half the aneuploid taxa included herein show chromosome counts greater than $n = 16$. One of these "higher level" aneuploids, *D. asterophora* var. *asterophora*, is interpreted as a tetraploid derived from a base number of $x = 10$. The other five appear to have originated through hybridization between aneuploids with lower base numbers and various euploid taxa. The putative parents of these five aneuploids belong to divergent, well-supported clades (Beilstein and Windham 2003), and hypotheses invoking hybridization between such distantly related species are almost without precedent in the genus. Previous reports of allopolyploidy in *Draba* (e.g., Brochmann et al. 1992b; Widmer and Baltisberger 1999) all involve closely related, exclusively euploid taxa. There is no evidence of natural, ongoing hybridization between divergent lineages in the genus, and Mulligan (1974, 1975) reports that attempts to cross distantly related species are rarely successful. And yet, such hybridization must have occurred in the past. In the three cases where I can reconstruct par-

entage with some degree of certainty (i.e., *D. argyrea, D. crassifolia* and *D. paucifructa*), the putative hybrids are intermediate in nearly every feature and show chromosome numbers that are perfectly additive. Although the exact origins of *D. hitchcockii* and *D. jaegeri* are less clear, Koch and Al-Shehbaz (2002) provide strong DNA evidence that they, too, arose through hybridization between divergent lineages. These data suggest that reticulation between major clades, previously thought to be rare in *Draba*, may have played an important role in the evolution of the genus.

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FACTORS AFFECTING SEED PRODUCTION BY THE ENDANGERED CHAPARRAL SHRUB *FREMONTODENDRON CALIFORNICUM* SUBSP. *DECUMBENS* (STERCULIACEAE)

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Abstract

Insect herbivory can greatly decrease plant reproductive success. This experiment reduced insect herbivore damage to branches of the federally endangered Pine Hill flannel bush (*Fremontodendron californicum* subsp. *decumbens*) during two flowering seasons to explore interactions among factors that can limit reproductive output (e.g., resource limitation, pollen limitation, seed predation). Experimental treatments included insecticide and control (water spray) treatments in 1983, with these and an insecticide plus exclosure treatment in 1984. Exclosures were designed to decrease herbivory of fruits by rodents. Reproductive stages (flower buds, flowers, and fruits) were counted and examined periodically for damage, and mature fruits were collected and seeds counted. In both years, insecticide treatment greatly decreased insect herbivory, increasing survival of flower buds, flowers, and fruits so that seed production increased 14- to 27-fold. Pollination success was unaffected by treatments, but fruit abortion increased significantly on insecticide-treated branches. Rodent herbivory of fruits greatly impacted fruit production on insecticide-treated branches in 1983, an El Niño-Southern Oscillation (ENSO) year, but was relatively unimportant in 1984 (a non-ENSO year). I concluded that: 1) seed output is limited by insect herbivores and can be greatly increased by insecticide treatment; 2) other limiting factors (resource limitation, rodent herbivory) increase in importance and partially compensate for increased fruit survival when insect herbivory is lessened by insecticide treatment; and 3) rodent fruit herbivory may be influenced by climate, being greater during years characterized by an ENSO event.

Key Words: El Niño-Southern Oscillation (ENSO), herbivory, insecticide, pollen limitation, resource limitation.

Most organisms have remarkably high reproductive potentials, but these potentials are decreased by many ecological factors. For plants, seed production and seed survival may be constrained by an array of limiting factors. These include resource limitation (Juenger and Bergelson 1997; Meléndez-Ackerman et al. 2000; Rathcke 2000), direct or indirect losses caused by herbivore damage to plants (Hoffman and Moran 1998; Marvier and Kareiva 1999; Adler et al. 2001; Fletcher et al. 2001; Maschinski 2001), destruction of seeds by seed predators (Boyd and Serafini 1992; Christian 2001), and failure of seeds or fruits to develop due to inadequate levels of pollination (Buchmann and Nabhan 1996; Johnson and Bond 1997; Timmerman-Erskine and Boyd 1999; Adler et al. 2001; Spira 2001). Managers of rare plant populations may seek to increase population size through manipulation of these limiting factors and, in some cases, dramatic increases in reproductive output may be achieved (e.g., Bevill et al. 1999). However, factors that limit plant reproduction often are interactive (Brody 1997), so that a change in one factor may change another. How factors that affect plant reproduction will interact is difficult to predict in a particular case, because of the importance of species-specific life history traits and also because of the unique ecological context that surrounds each plant species.

Herbivory is a constant threat to most plants (Harper 1977; Crawley 1983) and can limit the population size of some rare plants (e.g., Henriquez and Simonetti 2001). The herbivores in these cases may be native (Fletcher et al. 2001) or non-native (Henriquez and Simonetti 2001), vertebrate (Maschinski 2001) or invertebrate (Stanforth et al. 1997), but regardless are detrimental to reproduction and survival from the plant perspective. As noted by Bevill et al. (1999), relatively few studies have manipulated levels of insect herbivory on a rare plant species, and a simple yet direct method of doing so is through insecticide application. Small-scale insecticide application can reveal the role of insect herbivores in limiting plant populations (Harper 1977) but has been little used in studies of rare plants (Bevill et al. 1999). Small-scale insecticide applications can generate valuable information regarding rare plant population biology (Bevill et al. 1999). Insecticide application also may be a potential management tool for conservation of rare plant species that are subjected to large amounts of insect herbivore damage. This latter concept is controversial, as unintended negative side effects can occur from insecticide applications (Lesica and Atthowe 2000; Spira 2001). However, insecticide use may be appropriate under carefully defined and explored situations (Louda and Bevill 2000).

Fremontodendron californicum subsp. *decumbens*, listed as federally endangered in 1996 (U.S. Fish and Wildlife Service 1996), is a rare shrub endemic to El Dorado County in central California (Hickman 1993). This subspecies was listed as endangered for three reasons (U.S. Fish and Wildlife Service 1996). First, it has an extremely limited geographic distribution. All known individuals occur within ca. 2 km of the summit of Pine Hill (Boyd and Serafini 1992). Second, the total population size of this subspecies (<2,000) is relatively small (Boyd and Serafini 1992). Finally, burgeoning residential development in the vicinity of Pine Hill is fragmenting and destroying habitats surrounding populations of this species.

The largest losses to the reproductive potential of *F. californicum* subsp. *decumbens* are caused by herbivorous insect larvae (Boyd and Serafini 1992). Insect herbivory destroys approximately 98% of the flower buds, flowers, and fruits produced during a reproductive season. Boyd and Serafini (1992) suggested that elimination of insect herbivory could potentially boost seed production by as much as 100-fold. However, they also realized that other limiting factors could emerge if insect herbivory was reduced, so that it was difficult to predict realized seed output if insect herbivory were decreased.

This study experimentally lessened insect herbivory using insecticide application during two reproductive seasons, and lessened rodent fruit herbivory during one season using a rodent exclosure treatment. I also documented losses due to other limiting factors whose importance might change if insect herbivory is experimentally modified. These limiting factors included resource limitation (causing increased flower/fruit abortion), pollen limitation (reflected by increased numbers of unpollinated flowers), and rodent herbivory of fruits. Fortuitously, the two seasons studied varied greatly in their climatic regime. The first season of the study (1983) was characterized by an El-Niño Southern Oscillation (ENSO) event (Glanz 2001) and was relatively wet, whereas the second season (1984) was relatively dry (Boyd 1996). These climatic differences may have influenced experimental outcomes between these two seasons and they provide another variable that can be addressed by the study. This study addressed the following specific questions:

1) Can seed production by this endangered species be increased by insecticide treatment?;
2) Do interactions occur between insect herbivory and other limiting factors that can influence plant reproductive success?;
3) Does the relative importance of insect herbivore damage, and its interaction with other limiting factors, vary between years?; and,
4) What are the conservation implications of these results?

Methods

Study Species

Lloyd (1965) described *Fremontodendron decumbens* as a rare species found on Pine Hill, El Dorado County, California. This taxon is currently recognized by Hickman (1993) at the subspecific level as *F. californicum* (Torrey) Cov. subsp. *decumbens* (R. Lloyd) Munz. It was listed as federally endangered in 1996 (U.S. Fish and Wildlife Service 1996).

Boyd and Serafini (1992) characterized both pre- and post-dispersal reproductive attrition in this subspecies. Most of the reproductive potential of study plants was decreased by insects at two pre-dispersal stages. Flower buds were attacked by larvae of two moth species. Most of the damage was attributed to larvae of *Decodes* sp. near *catherineae* Powell (Tortricidae: Lepidoptera), but *Sparganothis senecionana* (Walsingham) (Tortricidae: Lepidoptera) also damaged flower buds (Boyd and Serafini 1992). Larvae of these species bored into the sides of flower buds and consumed their contents, moving to another bud when the current bud's contents were consumed or when it began to senesce. Overall, Boyd and Serafini (1992) estimated that these insects destroyed 78% of flower buds produced.

Once an open flower was pollinated and fruit development began, the ripening ovary was targeted by another insect herbivore, a possibly undescribed species in the genus *Chionodes* (Gelechiidae: Lepidoptera). Larvae of this moth bored through the pericarp into a developing fruit and fed upon the maturing seeds, inhabiting the fruit until the seeds were consumed or the fruit died, and then moving to another nearby fruit. Overall, Boyd and Serafini (1992) estimated that 81% of developing fruits died, and that most dead fruits (87%) were killed by damage attributable to *Chionodes* larvae. Thus, about 70% of developing fruits were destroyed by this pre-dispersal insect herbivore.

Later studies focussed on pollination and seed dispersal mutualisms as critical steps in the reproductive biology of *Fremontodendron*. Boyd (1994) described the dependence of this subspecies upon native polylectic bees for pollination, finding that flowers did not self-pollinate when insect visitation was prevented by exclosures. Bees were efficient at finding and pollinating flowers, so that fruit production was not pollen-limited. However, seed production was greater (by about 2-fold) for hand-pollinated flowers in comparison to bee-pollinated flowers, so that some pollen limitation was occurring (Boyd 1994).

Seed dispersal relies upon a native harvester ant, *Messor andrei* (Mayr), which is attracted to seeds by the presence of an elaiosome and carries seeds to its nest and associated waste midden (Boyd 1996). Movement of seeds away from parent plant canopies is beneficial because, after a fire stimulates seed germination (Boyd 1987), seedlings dis-

persed from a parent plant have a 2.4-fold greater chance for survival (Boyd 2001). This survival advantage stems both from a lessened probability of rodent seedling herbivory and a greater probability that a dispersed seed will germinate in a post-fire opening in the chaparral canopy (Boyd 2001).

Study Site

The study site is privately owned land located on the eastern boundary of the Pine Hill Ecological Reserve, a 97-ha site established to protect *F. californicum* subsp. *decumbens* and several other rare plant species found on Pine Hill (U.S. Fish and Wildlife Service 1996). The *Fremontodendron* population on the study site is the largest known on private land, as most known individuals are found within the boundaries of the reserve (Boyd personal observation). The study site is a rocky chaparral-covered ridge immediately east of the summit of Pine Hill. This location, corresponding to site 1 of Boyd and Serafini (1992), is dominated by *Adenostoma fasciculatum* along with some *Arctostaphylos viscida*. Scattered individuals of *Heteromeles arbutifolia, Rhamnus californica, Rhamnus ilicifolia, Toxicodendron diversilobum, Lepechinia calycina, Ceanothus lemmonii,* and *Pinus sabiniana* also contribute to the approximately 70% shrub/tree cover on this site (nomenclature from Hickman 1993). Outcrops of gabbrodiorite rock, characteristic of the Pine Hill formation (Hunter and Horenstein 1992), cover most of the remaining ground surface. Despite containing a large population of *F. californicum* subsp. *decumbens* (>60 individuals), cover of this species is <5% (Boyd and Serafini 1992).

1983 Insecticide Experiment

I selected pairs of branches on 23 shrubs, pruning back surrounding growth if needed to ensure that each branch touched no others (thus isolating treatments to target branches). In mid-March 1983, I randomly assigned either insecticide or water treatment to the branches in each pair. Insecticide treatment consisted of a 1.2% dilution (v:v) of a stock commercial formulation of Sevin® (Union Carbide) plus 1.6% (v:v) Dipel® (Du Pont). The active ingredient of Sevin is carbaryl (1-napthyl methylcarbamate) whereas the active ingredient of Dipel is *Bacillus thuringiensis* (Bt). Spray was applied using hand-held plastic spray bottles. During spraying, I placed a plastic sheet under and to the sides of insecticide-sprayed branches to minimize insecticide drift onto non-target branches (Kruger and Scholtz 1997). Starting in mid-March and every 2 wk thereafter until fruits matured, I thoroughly wetted each branch with spray. A possible side-effect of insecticide application is toxicity to bees (Spira 2001). Therefore, during the flowering season for *Fremontodendron* (late April–June), I sprayed branches either very early or very late in

the day (when bee activity was minimal) to avoid harming the pollinators upon which this species depends for successful fruit production (Boyd 1994).

At each treatment date and before spray treatments were applied, I counted the numbers of the reproductive stages (flower buds, flowers, and fruits) present on each branch. I removed dead and dying flower buds and placed them on foliage beyond the marked portion of each branch so that they would not be counted subsequently. By placing them on the same branch, I provided any insect larvae that remained inside the buds the opportunity to remain on that branch.

I marked open flowers at each census interval with small lengths of colored plastic-coated wire placed around the pedicels, with each color corresponding to a particular census date. Dead flowers and fruits were visually examined for evidence of the cause of their deaths. Dead flowers were divided into two mortality categories: 1) attack by insect larvae; and, 2) pollination failure. The "attack by insect larvae" category included a variety of damage patterns, ranging from feeding damage inflicted upon the ovary to that caused by unidentified lepidopteran larvae that spun webbing which kept closed the sepals of buds preparing to open while they consumed the stamens and ovary within. Pollination failure was deduced from dead flowers that were in apparently pristine condition, usually with large amounts of pollen remaining in their anthers, and which lacked any visible evidence of insect attack. These dead flowers were identical to those observed in an earlier study of pollination biology (Boyd 1994) in which pollinator exclosures prevented flowers from being pollinated.

Fruit mortality was also classified into several categories. Causes of fruit mortality included: 1) damage by insect larvae; 2) fruit abortion; and, 3) herbivory by rodents. The "damage by insect larvae" category included that caused by insects which consumed large sections of the fruit wall as well as damage caused by *Chionodes* larvae burrowing through the fruit wall into the locules (Boyd and Serafini 1992). Fruit abortion was judged to have occurred if a developing fruit died and no evidence of insect damage could be observed. Rodent herbivory was deduced directly from the presence of bitten-off pedicels and indirectly from disappearance of fruits nearing maturity. Fruit disappearance was only attributed to rodent herbivory if other evidence of rodent attack (e.g., bitten-off pedicels, torn-open fruits) was found at that branch at that census date. Bitten-off pedicels were counted and removed so that they would not be counted again at the next census date. At the time of year at which marked fruits disappeared from branches and I found bitten-off pedicels on branches, I also found beneath nearby shrub canopies piles of fruits that had been peeled open and the seeds destroyed. In a number of instances the wire twists remained wrapped around the pedicels, providing clear evi-

dence of rodent herbivory upon fruits originating from treated branches.

I removed mature fruits (defined as dehiscing capsules) from branches as they became dry and counted the number of seeds in each fruit. Seeds were considered mature when full-sized and a deep ebony color. Tan or brown seeds invariably lack a healthy-appearing embryo (Boyd and Serafini 1992; Boyd 1994) and so such seeds were not counted.

1984 Insecticide and Rodent-Exclusion Experiment

In 1984 I conducted an experiment similar to that done in 1983, except that I selected three branches on each of 20 shrubs and randomly assigned three treatments to them: insecticide; insecticide plus rodent exclosure; and water-sprayed control. Insecticide treatments in 1984 consisted of Sevin® only, using a 0.39% (v:v) dilution of the stock commercial formulation. Dipel was not used in 1984 because I believed that Sevin alone was capable of controlling insect herbivory. Spraying commenced the first day buds were counted (mid-April 1984), but rodent exclosures were not installed over branches until after blooming had ceased (late June) so that rodent exclosures would not interfere with pollinator activity. Rodent exclosures were cylinders of 2.5 cm-mesh poultry wire, fastened around the branches so that enclosed developing fruits were at least 5 cm inside the wire.

Summary of Data Collected from Experimental Branches

For both the 1983 and 1984 experiments, I estimated the total production of flower buds on each branch. I did this for each branch by counting the live and dead flower buds found at each census date and adding that sum to the total number of dead buds found prior to that time. The largest number generated in this way from all census dates was used as an estimate of total flower bud production for each branch. Because dead buds were removed at each census, this provided a minimum estimate of total bud production by each branch. Total production of flowers and fruits was more directly determined because they were individually marked at each census date with colored wire.

In 1984, after seeds were extracted from mature fruits, mean seed mass was determined for a subsample of seeds from each experimental treatment. One hundred seeds were arbitrarily selected from each treatment and individually weighed to the nearest 0.1 mg.

Data Analysis

Data from each year were analyzed separately by one-way analysis of variance (ANOVA). Count and seed mass data were log-transformed, and percent data were transformed using an arcsine square root function, before statistical analysis to better-meet ANOVA assumptions (Zar 1996). I used a random effects model ANOVA in StatView 5.0 (Abacus Concepts 1998) to analyze counts of flower buds, flowers, fruits, mature fruits, and seeds per branch for both 1983 and 1984 data sets. Additional variables were calculated using the data collected from each branch and analyzed by randomized complete block design ANOVAs (Zar 1996) for both the 1983 and 1984 experiments. The latter ANOVA design was used to help isolate variation due to treatments from variation between sets of branches. For the 1984 experiment (which had three treatments), Fisher's Protected Least Significant Difference (PLSD) test was used for post-hoc means separations (at $\propto$ < 0.05) when ANOVA indicated that treatment effects were statistically significant. Variables analyzed in this manner included: insect-destroyed flower buds/flower bud (%), flowers produced/flower bud (%), failed pollination flowers/flower (%), insect-destroyed flowers/flower (%), fruits/flower (%), rodent-destroyed fruits/fruit (%), aborted fruits/fruit (%), mature fruits/fruit (%), seeds/flower bud, seeds/flower, seeds/fruit, and seeds/mature fruit. Since cause of mortality could not be determined for all reproductive stages that were counted, percentage values of the fates for a particular type of reproductive stage (flowers, fruits, etc.) usually did not sum to 100%. However, this approach still allowed relative comparisons to be made between treatments so that the magnitude of treatment effects on these variables could be determined.

RESULTS

Effects of Treatments on Production of Flower Buds, Flowers, Fruits, Mature Fruits, and Seeds

Insecticide and insecticide plus exclosure treatments increased the numbers of most reproductive stages (relative to control treatments) during both years the experiment was conducted (Table 1). Only flower bud production was unaffected by treatments, a result observed for both year's experiments. Flower, fruit, mature fruit, and seed numbers were significantly increased by insecticide treatment (Table 1). Relative differences in reproductive output between control and experimental treatments increased for later reproductive stages (Fig. 1). For example, 1983 flower production of insecticide-treated branches was 3.0-fold that of control branches, but fruit production was 8.2-fold that of control branches (Fig. 1). In general, the effectiveness of insecticide treatment was greater in 1984. This is shown by the increase in ratios between insecticide- and control-treated branches in 1984 (Fig. 1). For example, in 1984 fruit production was 5.1-fold greater for branches receiving the insecticide treatment, whereas this value was only 3.0-fold greater in 1983. The rodent exclosure treatment (added in the 1984 experiment) did not sig-

TABLE 1. MEAN PRODUCTION OF REPRODUCTIVE UNITS PER BRANCH BY BRANCHES RECEIVING EXPERIMENTAL TREATMENTS (SE IN PARENTHESES). Data from the 1983 and 1984 experiments were analyzed by separate random effects model one-way ANOVAs. For each year's experiment, the ANOVA result is presented for each reproductive stage. Values for the 1984 experiment with differing superscripts indicate treatment means that differ significantly ($\alpha < 0.05$: Fisher's PLSD test).

Reproductive stage	1983 Experiment (N = 23)			1984 Experiment (N = 20)			
	Control	Insecticide	ANOVA	Control	Insecticide	Insecticide/ Exclosure	ANOVA
Flower buds	65[a] (6.9)	71[a] (9.5)	0.94	74[a] (8.4)	70[a] (6.2)	80[a] (9.6)	0.98
Flowers	17[a] (3.6)	51[b] (6.9)	0.0002	18[a] (4.4)	67[b] (6.3)	73[b] (9.3)	<0.0001
Fruits	9.5[a] (1.9)	33[b] (4.2)	<0.0001	11[a] (3.5)	61[b] (5.6)	66[b] (8.3)	<0.0001
Mature fruits	0.61[a] (0.20)	5.0[b] (1.9)	0.001	1.9[a] (0.70)	32[b] (5.0)	41[b] (5.5)	<0.0001
Seeds	1.2[a] (0.41)	17[b] (6.8)	0.0012	4.7[a] (2.0)	110[b] (19)	126[b] (18)	<0.0001

nificantly increase fruit or seed production beyond that attributable to insecticide treatment alone (Table 1, Fig. 1).

Effects of Treatments on Flower Bud Fates

Counts of flower buds did not significantly differ between control and treated branches in either 1983 or 1984 (Table 1). However, flower bud mortality
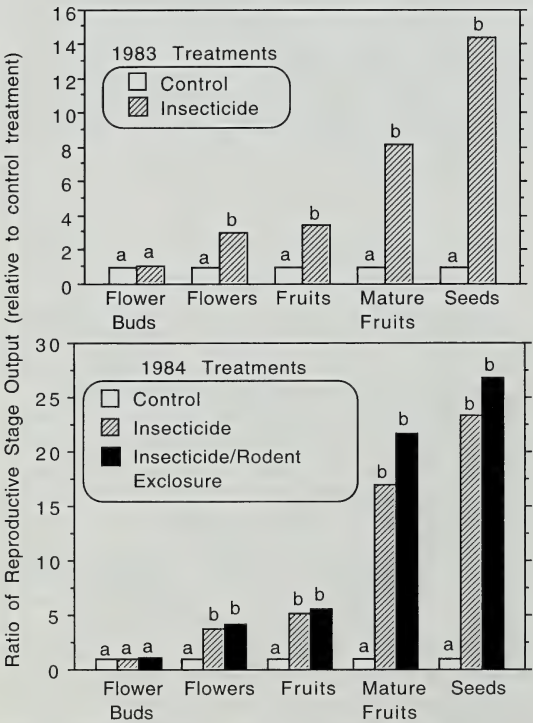
FIG. 1. Effects of treatments on production of reproductive stages by experimental branches. Counts are expressed relative toc the control for each year's experiment. Different letters denote significantly different comparisons between treatments (from statistical analyses presented in Table 1) for each reproductive stage (flower buds, flowers, etc.).

was significantly decreased by insecticide treatment in both years. For the 1983 experiment, almost seven-fold more insect-destroyed buds were counted on control branches compared to pesticide-treated branches. Mean percentages of insect-destroyed flower buds/bud (SE in parentheses, N = 20) were 48% (5.8%) for control and 7.0% (1.6%) for insecticide treatments (ANOVA; P < 0.0001). In 1984, the difference in the percentages of insect-destroyed flower buds between control and insecticide treatments increased to about 15-fold. Mean percentages of insect-destroyed flower buds/bud (SE in parentheses, N = 23) were 70% (3.4%) for control branches, 4.7% (0.90%) for insecticide branches, and 4.5% (0.70%) for insecticide/rodent exclosure branches. These means differed significantly (ANOVA; P < 0.0001). Fisher's Protected Least Significant Difference (PLSD) test ($\alpha < 0.05$) revealed that control branches differed significantly from branches treated with insecticide, but insecticide/rodent exclosure branches did not differ from those treated with insecticide alone. This is unsurprising because the rodent exclosure treatment was added after flowering had ceased. However, it does show that insecticide and insecticide/rodent exclosure branches were similar to each other at the time rodent exclosures were installed.

Effects of Treatments on Flower Fates

As a result of greater flower bud survival, more than twice as many flowers were produced (per flower bud initiated) on insecticide-treated branches in 1983 (Table 2). Similar results were observed in 1984: more flowers were produced per flower bud (about 4-fold more) when branches were insecticide-treated (either insecticide or insecticide/rodent exclosure treatments; Table 2). Relatively few flowers experienced pollination failure during either year's experiment, and no significant treatment effects on this variable were observed in either year (Table 2). Values for this parameter in 1983 were 8% or less for both treatments, and in 1984 were < 6% for all three treatments (Table 2). Treatment effects on the percentage of insect-destroyed flow-

TABLE 2. MEAN VALUES OF FLOWER PARAMETERS (SE IN PARENTHESES) FROM THE 1983 AND 1984 EXPERIMENTS. ANOVA result for each variable is the P-value for the treatment main effect. Differing superscripts for the means from the 1984 experiment denote statistically different means (Fisher's PLSD test, $\alpha < 0.05$).

Parameter	Control	Insecticide	Insecticide/ Exclosure	ANOVA
1983 experiment (N = 23 except where noted)				
Flowers/flower bud (%)	26 (4.9)	69 (4.0)	—	<0.0001
Failed pollination flowers/flower (%)	5.6 (1.8), N = 19	8.0 (2.9)	—	0.56
Insect-destroyed flowers/flower (%)	18 (4.6), N = 19	6.7 (1.7)	—	0.076
1984 experiment (N = 20 except where noted)				
Flowers/flower bud (%)	21[a] (4.0)	95[b] (3.2)	91[b] (2.1)	<0.0001
Failed pollination flowers/flower (%)	5.1 (1.8), N = 19	4.3 (0.90)	5.5 (1.3)	0.56
Insect-destroyed flowers/flower (%)	38[a] (6.4), N = 19	1.5[b] (0.70)	1.5[b] (2.6)	<0.0001

ers differed between years. In 1983, insect-destroyed flowers were more abundant on control branches, but ANOVA showed this difference was only marginally significant (P = 0.076; Table 2). Results for 1984 showed a highly significant decrease in flowers destroyed by insects when branches were treated with insecticide (P < 0.0001). About 25-fold more insect-destroyed flowers were counted on branches receiving the control treatment, when compared to those receiving either insecticide or insecticide/rodent exclosure treatments (Table 2).

The rodent exclosure treatment in 1984 did not significantly affect flower mortality (Table 2). Fisher's PLSD test ($\alpha < 0.05$) revealed that the mean number of flowers/flower bud for the control treatment differed significantly from that for branches treated with insecticide, but the insecticide/rodent exclosure treatment mean did not differ from the mean for insecticide treatment alone. This is expected because the rodent exclosure treatment was added after flowering ceased, but it does show that all insecticide-treated branches were responding similarly to the insecticide treatment at that point in the experiment.

Effects of Treatments on Fruit Fates

The greatest differences between the outcomes of the 1983 and 1984 experiments were observed for the fruit stage (Table 3). In 1983, fruit production per flower was statistically similar for both treatments, although the mean for insecticide-treated branches was 1.2-fold that of the controls (Fig. 1). In contrast, for the 1984 experiment, fruit set per flower on insecticide and insecticide/rodent exclosure branches was extensive (ca. 90% for both treatments) compared to that of control branches (ca. 50%). This difference was highly significant (Table 3).

Rodent herbivory differed greatly between years. In 1983, the percentage of fruits destroyed by rodents was 3.5-fold greater for pesticide-treated branches. In contrast, relatively little rodent herbivory occurred during 1984 (Table 3). Rodents destroyed only 8.8% of fruits on control branches and 13% of those on insecticide-treated branches, compared to 53% for insecticide-treated branches in 1983. Rodent exclosures effectively eliminated rodent herbivory of fruits on insecticide/rodent exclosure branches during 1984, although a few fruits

TABLE 3. MEAN VALUES OF FRUIT PARAMETERS (SE IN PARENTHESES) FROM THE 1983 AND 1984 EXPERIMENTS. ANOVA result for each variable is the P-value for the treatment main effect. Differing superscripts for means from the 1984 experiment denote statistically different means (Fisher's PLSD test, $\alpha < 0.05$).

Reproductive stage	Control	Insecticide	Insecticide/ Exclosure	ANOVA
1983 experiment (N = 23 except where noted)				
Fruits/flower (%)	57 (4.5), N = 19	70 (4.7)	—	0.22
Insect-destroyed fruits/fruit (%)	52 (7.6), N = 19	2.8 (1.1)	—	<0.0001
Rodent-destroyed fruits/fruit (%)	15 (5.1), N = 19	53 (6.4)	—	<0.0001
Aborted fruits/fruit (%)	12 (3.7), N = 19	22 (4.9)	—	0.055
Mature fruits/fruit (%)	11 (5.6), N = 19	17 (5.3)	—	0.11
1984 experiment (N = 20 except where noted)				
Fruits/flower (%)	54[a] (6.9), N = 19	91[b] (1.3)	90[b] (1.3)	<0.0001
Insect-destroyed fruits/fruit (%)	46[a] (8.9), N = 17	0.40[b] (0.20)	0.60[b] (0.20)	<0.0001
Rodent-destroyed fruits/fruit (%)	8.8[a] (3.7), N = 17	13[a] (3.9)	0.10[b] (0.10)	0.0032
Aborted fruits/fruit (%)	16[a] (5.3), N = 17	35[b] (4.3)	34[b] (4.1)	<0.0001
Mature fruits/fruit (%)	30[a] (9.1), N = 17	50[b] (4.3)	65[b] (4.2)	0.0042

TABLE 4. MEAN VALUES OF SEED PARAMETERS (SE IN PARENTHESES) FROM THE 1983 AND 1984 EXPERIMENTS. ANOVA result for each variable is the P-value for the treatment main effect. Differing superscripts for means from the 1984 experiment denote statistically different means (Fisher's PLSD test, α < 0.05).

Parameter	Control	Insecticide	Insecticide/Exclosure	ANOVA
1983 experiment (N = 23 except where noted)				
Seeds/flower bud	0.016 (0.0050)	0.27 (0.092)	—	0.0014
Seeds/flower	0.089 (0.040), N = 19	0.42 (0.16)	—	0.24
Seeds/fruit	0.21 (0.11), N = 19	0.58 (0.25)	—	0.18
Seeds/mature fruit	1.8 (0.19), N = 8	2.9 (0.49), N = 16	—	0.42
1984 experiment (N = 20 except where noted)				
Seeds/flower bud	0.050[a] (0.020)	1.6[b] (0.29)	1.8[b] (0.23)	<0.0001
Seeds/flower	0.33[a] (0.12), N = 19	1.7[b] (0.28)	2.0[b] (0.27)	<0.0001
Seeds/fruit	0.91[a] (0.37), N = 17	1.8[b] (0.29)	2.2[b] (0.28)	0.0003
Seeds/mature fruit	2.4 (0.44), N = 12	3.6 (0.45)	3.1 (0.26)	0.14
Seed mass (mg, N = 100)	26.6[a] (0.28)	29.1[b] (0.37)	28.4[b] (0.33)	<0.0001

were close enough to the sides of some exclosures to be reached by rodents and hence some rodent herbivory (0.10%) was recorded for exclosed branches (Table 3).

Other causes of fruit mortality were affected in similar ways by treatments in both years. Insecticide treatment was very effective at decreasing fruit mortality caused by insects: in 1983 the percentage of insect-destroyed fruits was 18.5-fold greater for the control treatment (Table 3). In 1984, insect-destroyed fruits were considerably more abundant on control branches (ca. 92-fold; Table 3). Insecticide treatment also resulted in greater fruit abortion in both years. In 1983, the percentage of aborted fruits was greater for pesticide-treated branches, although the difference was only marginally significant (Table 3). In 1984, aborted fruits were significantly more abundant on insecticide and insecticide/rodent exclosure branches (ca. 2-fold; Table 3).

Due to interactions between the above causes of mortality, the effect of treatments on mature fruit production varied between years. In 1983, when rodent herbivory was intense, the production of mature fruits (expressed as % mature fruits/initiated fruit) did not differ due to insecticide treatment (Table 3). The following year, when rodent herbivory was much decreased, the percentage of mature fruits produced (per fruit initiated) was significantly greater (by 1.5- to 2-fold) for branches receiving either insecticide or insecticide/rodent exclosure treatments (relative to the control: Table 3).

Effects of Treatments on Seed Production and Seed Mass

Experimental treatments boosted seed production in both years (Fig. 1, Table 1) but, when measures of seed production are expressed relative to numbers of other reproductive stages, the results vary between years (Table 4). In 1983, there was a statistically significant treatment effect only for seeds/flower bud (Table 4), when approximately 17-fold more seeds were produced per flower bud on in-

secticide-treated branches. When seed production was expressed relative to flower, fruit, or mature fruit production, no significant treatment effects resulted (Table 4). In contrast to 1983, data from 1984 showed significant treatment effects for almost all seed-based parameters. Significant increases in seeds/flower bud, seeds/flower, and seeds/fruit were documented in 1984 in response to insecticide and insecticide/rodent exclosure treatments (Table 4). Only for seeds/mature fruit did treatments have no effect in 1984, a result also observed in 1983 (Table 4).

Seed mass was measured in 1984 and also differed significantly due to treatments (Table 4). Mean seed mass from insecticide and insecticide/rodent exclosure branches was slightly greater (by ca. 8%) than for seeds from control branches.

DISCUSSION

Manipulative studies of plant reproductive biology are useful because they can expose interactions between the many factors that affect plant reproduction (Harper 1977; Brody 1997; Bevill et al. 1999). For *F. californicum* subsp. *decumbens,* the observational study of Boyd and Serafini (1992) showed that only 1.8% of flower buds became mature fruits, with insect herbivory causing the vast majority of the loss. They estimated that elimination of insect herbivory could boost seed output up to 100-fold as long as other limiting factors would not increase in compensation. In this manipulative study, seed production increased 14-fold (1983) and 25-fold (1984) due to insecticide treatment. These are very large increases, but are much less than the potential increase calculated by Boyd and Serafini (1992). Thus, other limiting factors increased in importance as insect herbivore damage decreased.

Resource limitation was one factor that counteracted the lessened insect-caused mortality of reproductive stages on insecticide-treated branches. Aborted fruits were marginally more abundant on insecticide-treated branches in 1983 but were great-

ly increased in 1984 on insecticide-treated branches relative to the control (Table 3). This increase in the abortion rate in 1984 is associated with increased fruit set in that year as well. In 1983, insecticide branches had 3.5-fold more fruits than controls while in 1984 insecticide treatment boosted fruit numbers 5.1- to 5.5-fold (Fig. 1). The increase in fruit abortion in 1984 is consistent with resource limitation becoming more severe when fruit production is increased.

Rodent herbivory also counteracted decreased insect herbivory on insecticide-treated branches, but it varied greatly in magnitude between years. In 1983, rodent herbivory greatly decreased fruit survival and was disproportionately concentrated on insecticide-treated branches (Table 3). This implied that rodents were responding to the greatly elevated density of fruits on these branches (3.5-fold that of control branches: Table 1, Fig. 1). In 1984, rodent herbivory was practically eliminated by the exclosure treatment yet rodent herbivory was a minor contributor to fruit mortality for all treatments that year (Table 3). Fruit density was greater on insecticide-treated branches in 1984 than in 1983 (Table 1, Fig. 1), but rodent herbivory was much less. Thus, the density-dependent response of rodents to fruits observed in 1983 does not explain the results from 1984. I suggest that this difference in rodent response is associated with the ENSO event of 1982–1983.

The two seasons included in this study varied dramatically in climate. California experienced the effects of an ENSO event during 1982–1983 (Glanz 2001) but 1983–1984 was relatively dry. In general, precipitation in California during 1982–1983 greatly increased and the cool rainy spring of 1983 delayed plant blooming and fruit maturation. Total precipitation at the weather station nearest to Pine Hill (Placerville, 16 km NE of Pine Hill) was 202% of the long-term average in 1983 but only 74% of average in 1984 (Boyd 1996). Boyd (1996) noted the effect of this ENSO on the phenology of *Fremontodendron* during a 5-yr census of fruit maturation times (extending from 1982–1986). Fruit maturation was delayed by at least 10 d in 1983 compared with 1984 (Boyd 1996). Delayed fruit maturation also was documented in this study. The last fruits to mature on experimental branches were collected on 16 September in 1983 but on 20 August in 1984. I suggest that this change in phenology made fruits available to rodents at an unusual time of the year in 1983, a time of the year in which they were in need of food and took advantage of the availability of *F. californicum* subsp. *decumbens* fruits. Rodent damage was much less in 1984 because fruits matured much earlier during that year. Most rodent damage in 1983 was observed during mid-July to early August whereas, in 1984, most fruits had already matured by that time. Thus, rodent herbivory may have interacted with climate fluctuation to produce a more complicated pattern

of reproductive outcomes. Such interactions of climate and factors that determine plant reproductive output are probably common but are in need of explicit study (Brody 1997).

Other factors that might have interacted with the decreased insect herbivory of insecticide-treated branches to change their reproductive output did not change significantly. One of these was pollen limitation. Flowers of this species do not self-pollinate and require an insect visit for pollination (Boyd 1994). In the current study, the increased density of flowers on insecticide-treated branches did not significantly change the proportion of "pollination failure" flowers counted (Table 2). This implies that bees responded to increased floral density in compensation for greater floral availability. The major bee species that visit *F. californicum* subsp. *decumbens* are generalists (Boyd 1994). They may have increased their foraging on flowers of this species in response to the increase in resources created by increased floral density.

Another feature that did not respond to insecticide-caused changes in flower and fruit density was total flower bud production per branch. Some plants exhibit reproductive compensation for herbivore losses, initiating more flower buds to replace those lost to herbivory (e.g., Juenger and Bergelson 1997). *Fremontodendron* did not respond in this way, as total flower bud production was similar for insecticide-treated and control branches (Table 1, Fig. 1). This is probably explained by the seasonal growth pattern of this species. Flower buds are produced in the axils of leaves during the flush of stem growth that occurs in spring. Thus, flower buds are initiated only at that time and, once stem growth ceases in late spring (when bud losses from insect predation continue to increase), there is no opportunity to produce additional flower buds to replace those destroyed. However, longer-term compensation (i.e., that occurring in the next flowering season) is possible (e.g., Meléndez-Ackerman et al. 2000) but unexplored in this case.

Besides characterizing factor interactions, this manipulative study uncovered a previously unreported cause of *Fremontodendron* fruit mortality. Boyd and Serafini (1992) did not detect pre-dispersal rodent herbivory of fruits during their study. Thus, its occurrence in the 1983 experiment was a surprise and the addition of an exclosure treatment in the 1984 experiment was an attempt to manipulate rodent herbivory as well as insect herbivory. The identity of the rodent herbivore is unknown because I never directly observed removal of fruits by rodents from study branches. However, once (August 1983) I observed a California ground squirrel (*Citellus beecheyi*), a diurnal rodent species, opening near-ripe fruits of *Fremontodendron* on the study site. I also fed fruits to several *C. beecheyi* at a site in the Pine Hill Ecological Reserve; they left behind fragments similar to those found in piles under study branches on the study

site. Thus, the available evidence points to *C. beecheyi* as the rodent fruit herbivore. However, nocturnal rodents also consume *Fremontodendron* seeds (Boyd and Serafini 1992) and these might have attacked fruits nearing maturity. Regardless of the identity of this rodent herbivore species, detection of its impact was facilitated by the insecticide treatment. By greatly increasing fruit set, insecticide treatment made apparent the losses due to rodent fruit herbivory, as many large marked fruits were removed from these branches as they matured. Thus, as suggested by Harper (1977), manipulative studies have the potential to uncover previously unrecognized factors that may be important to the biology of a particular plant species. Such studies therefore can be valuable to managers of rare plant species.

Global climate change will have profound effects on Earth's biota (Pounds and Crump 1994; Markham 1996; McCarty 2001; Wilson 2002), including rare species (Brown et al. 1997; Saetersdal and Birks 1997). Multi-year studies of rare species that include years with markedly varying climate may give insight into the challenges faced by rare species in response to global climate change. In this study, rodent herbivory may have been affected by climate, with greatly increased rodent fruit herbivory observed during an ENSO year. Similar reports of negative consequences of ENSO events for plants (e.g., Harrison 2000) merit concern, as the frequency of ENSO events is predicted to increase as a consequence of global warming (Timmermann et al. 1999). On the other hand, the climate difference between these years apparently did not affect other aspects of *Fremontodendron* reproduction. For example, pollination success did not differ between 1983 and 1984. As with fruit maturation, there was a phenological shift in flowering time. The last open flowers on the study branches were marked on 21 July in 1983 but on 4 July in 1984. The lack of a negative pollination effect is heartening because the pollination biology of this species is vulnerable to disruption. Reliance of *Fremontodendron* on generalist bees means that its pollination success is contingent on the ecological context of the Pine Hill floral community. If more attractive flowers of other species are available to bees, and if flowers are a limiting resource for them, then pollinator service to this endangered species may decline. Boyd (1994) pointed out that flowers of *Fremontodendron* are fortunately relatively large and resource-rich, making them relatively attractive in the context of co-occurring chaparral species.

This experiment showed that insecticide application has the potential to greatly boost seed production by *F. californicum* subsp. *decumbens*. Although it must be pointed out that whole-plant responses to insecticide treatment may vary from branch-level responses, it is clear that insecticide application would nevertheless allow greater seed production. However, other features of this species ensure that insecticide treatment alone will not be sufficient to increase plant numbers over short ecological time-scales. Boyd and Serafini (1992) and Boyd (2001) demonstrated that *Fremontodendron* seeds are dormant until the seed coat is scarified by fire. Thus, increased seed production would likely cause increased input of seeds into the seed bank, but no seedlings would result until after a fire occurred. Increasing development in the area surrounding the Pine Hill Ecological Reserve (U.S. Fish and Wildlife Service 1996) may discourage the use of fire as a management tool on the reserve and extend the interval between prescribed fires. This would decrease the frequency of recruitment events for the *Fremontodendron* population.

Just as density-dependent interactions can occur between factors that influence pre-dispersal seed production, so can they occur between pre- and post-dispersal factors. Boyd and Serafini (1992) found that 90% of *Fremontodendron* seeds released into the litter beneath parent shrub canopies were destroyed by rodents within one year. These rodents may respond in a positive density-dependent manner to increased seed production and destroy a greater percentage of the seeds produced, thus decreasing the effectiveness of increased seed output by insecticide-treated shrubs.

It is worth noting that pollination mutualisms were not noticeably affected by insecticide treatment in this study. Negative effects could have occurred, either by direct effects or by indirect effects. Spira (2001) pointed out that insecticides may directly threaten pollination mutualisms of rare plants by killing pollinating insects. Indirect effects may also occur, such as if increased flower production on treated branches dilutes the activities of pollinators and decreases the probably of visitation to a single flower. However, unpollinated flowers were not significantly more abundant on insecticide-treated branches in this study. Thus, no negative impacts of insecticide treatment were apparent from the plant perspective in this case.

Large-scale insecticide use might be an inappropriate tactic because of negative impacts of insecticide on non-target organisms (Lesica and Atthowe 2000). In this case, one target insect herbivore may itself be worthy of conservation. Fruits of *F. californicum* subsp. *decumbens* are attacked by larvae of a *Decodes* species that may be an undescribed taxon (Boyd and Serafini 1992). To my knowledge, the taxonomic status of this insect herbivore is still unresolved but this situation has two implications. First, some groups of organisms are still poorly known even in relatively well-studied countries such as the United States (e.g., Schaefer 1990; Bossart and Carlton 2002). Thus, basic taxonomic research is still vitally important to global conservation efforts (Green 1998; Wilson 2002). Second, potential conflicts between the needs of rare plants and rare herbivores that may feed upon those plants

can occur (e.g., Simon et al. 2001). Lesica and At-thowe's (2000) suggestion that natural predators be substituted for insecticide as a management tool to control detrimental insect herbivory to rare plants does not obviate the dilemma in this case. Unfortunately, as the biodiversity crisis deepens (Wilson 2002), situations in which managers must choose between the conflicting and simultaneous needs of multiple rare species are certain to increase.

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TWO SPECIES OF *PASSIFLORA* (PASSIFLORACEAE) IN THE SONORAN DESERT AND VICINITY: A NEW TAXONOMIC COMBINATION AND AN INTRODUCED SPECIES IN ARIZONA

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Abstract

Two species of *Passiflora* in Arizona and northwestern Mexico are investigated. One species, *P. arida,* native to Baja California and Sonora, has recently been found to be naturalizing in southern Arizona. Another, *P. foetida* var. *arizonica,* native to southern Arizona and Sonora, is examined for taxonomic distinctiveness and raised to a new species, **Passiflora arizonica**. These two species are compared to each other, the potential threat of weediness in *P. arida* is reviewed, and the distinctive features of the biology of *P. arizonica* are discussed. Furthermore, comparisons are made with several other related New World *Passiflora* species of similar geographic range or morphology.

Resumen

Dos especies de *Passiflora* en Arizona y el noreste de México están siendo investigadas. Una especie, *P. arida,* nativa de Baja California y Sonora, ha sido recientemente encontrada naturalizada en el sur de Arizona. Otra, *P. foetida* var. *arizonica,* nativa del sur de Arizona y Sonora es examinada para su distinción taxonómica y como nueva especie, *P. arizonica.* Estas dos especies son mutuamente comparadas, la potencial amenaza de invasión en *P. arida* es revisada y la distinta caracterización biológica de *P. arizona* son discutidas. Además, se hacen comparaciones con otras especies de *Passiflora* del Nuevo Mundo de rango geográfico o morfología similar.

Key Words: *Passiflora,* Sonoran Desert, Arizona, Mexico, weed, taxonomy, *Dysosmia.*

Of worldwide distribution in tropical to warm temperate regions, the genus *Passiflora* contains close to 500 species (Vanderplank 2000), with many species popular in cultivation. Within the continental United States there are thirteen native species (Killip 1938). In Arizona there are three native species, *P. bryonioides* HBK., *P. foetida* L. var. *arizonica* Killip and *P. mexicana* Juss. (Killip 1938; Tidestrom and Kittell 1941; Kearney and Peebles 1942; Kearney and Peebles 1951; Shreve and Wiggins 1964; MacDougal 2001). In northwestern Mexico (for the purpose of this paper consisting of Baja California, Baja California Sur, Chihuahua, northern Sinaloa and Sonora) there are the same species plus *P. arida* (Mast. and J.N. Rose) Killip, *P. foetida* L. var. *gossypiifolia* (Ham.) Mast., *P. fructicosa* Killip and *P. palmeri* J.N. Rose var. *palmeri.* However, *P. arida* (Mast. and Rose) Killip has appeared relatively recently in Arizona but has nearly avoided detection until the last two years (MacDougal 2001) and the rapidity of its spread suggests that it has the potential to become a problematic weed. This species had avoided detection in Arizona because it was typically identified as *P. foetida* L. var. *arizonica.* Upon further examination of the latter species in herbarium specimens, in the

field and with cultivated plants, it was determined that it merited recognition as a distinct species. A new combination is presented here, *P. arizonica* (Killip) D.H. Goldman. This paper is an outgrowth of, and necessary foundation for my work on the treatment of the genus for the Flora of North America (FNA) project, to be published in the next few years.

Although this paper addresses some taxonomic issues within the subgenus *Dysosmia* (DC.) Reichb., it is not intended to address definitively the numerous uncertainties within this subgenus, nor is it a monograph, particularly of the diverse and widespread *P. foetida.* Killip (1938), Standley and Williams (1961), Vanderplank (2000) and MacDougal and McVaugh (2001) discussed the significant and overall taxonomic difficulties with the subgenus, particularly in *P. foetida,* and MacDougal and McVaugh (2001) review some of the complicated variation in this species in southwestern Mexico. *Passiflora foetida* alone has 38 recognized varieties by Killip (1938), who uses characters such as geographic distribution and ovary pubescence to distinguish between several of these. MacDougal and McVaugh (2001) express doubt about the value of ovary pubescence as a useful taxonomic character in *P. foetida,* and some plants of uncertain identity in cultivation at Cornell University (my collections *1768, 1773, 1793* and *2158;* see Specimens Examined) either are completely

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glabrous both florally and vegetatively with the exception of some glandular trichomes, or otherwise identical in every way but covered with a dense indumentum of eglandular trichomes. This subgenus has an abundance of morphologically intermediate specimens between different species or varieties. There are apparent geographic (and often undescribed) variants and races of widespread taxa, species that appear less distinct from *P. foetida* than some of the varieties of the latter, and an apparent loss of good morphological characters in dried, pressed specimens. This all would suggest that subgen. *Dysosmia* contains some of the most complicated taxonomic problems in the genus. In its great majority this hideous taxonomic pageant is beyond the scope of this paper, where only the relevant members of subgen. *Dysosmia,* those bearing similar morphology and/or geography to the two taxa of interest, are evaluated for distinctiveness.

METHODS

For this study, observations and measurements were made from both living and pressed material. *Passiflora* specimens in the subgenus *Dysosmia* were examined, primarily from Arizona and northwestern Mexico. To evaluate better the complexity of this subgenus relative to the geographic region of primary focus here, specimens were also examined from Texas, the entirety of Mexico, portions of adjacent Central America, Argentina and Paraguay. Measurements were made most intensively from *P. arida* and *P. foetida* var. *arizonica,* as these species are pertinent to the scope of FNA and the State of Arizona, although measurements were also made from other taxa. Morphological descriptions are provided here only for those taxa of primary interest and are provided based on morphological observations from cultivated and herbarium material and the work of Killip (1938), Shreve and Wiggins (1964) and Wiggins (1980). Taxa of primary interest were *P. arida* and *P. foetida* var. *arizonica;* those of necessary interest based on overlapping geographic ranges were *P. foetida* var. *gossypiifolia, P. fruticosa* and *P. palmeri;* and those of necessary comparison due to putatively similar morphology were *P. chrysophylla* Chodat, *P. foetida* var. *gossypiifolia, P. foetida* var. *hibiscifolia* (Lam.) Killip, *P. foetida* var. *nigelliflora* (Hook.) Mast., *P. foetida* var. *oaxacana* Killip, *P. santiagana* (Killip) Borhidi (=*P. foetida* var. *santiagana* Killip), *P. foetida* var. *subpalmata* Killip and *P. foetida* var. *vitacea* Mast. Other taxa evaluated for comparison were superficially similar varieties of *P. foetida* from Mexico and nearby within Central America, specifically, *P. foetida* var. *acapulcensis* Killip, *P. foetida* var. *ciliata* (Aiton) Mast., *P. foetida* var. *foetida, P. foetida* var. *hastata* (Bertol.) Mast., *P. foetida* var. *hirsutissima* Killip, *P. foetida* var. *lanuginosa* Killip, *P. foetida* var. *longipedunculata* Killip (possibly no more than a form of var. *gossypii-*

folia; see MacDougal and McVaugh 2001), *P. foetida* var. *maxonii* Killip, *P. foetida* var. *nicaraguensis* Killip, *P. foetida* var. *parvifolia* Killip, *P. foetida* var. *salvadorensis* Killip and *P. foetida* var. *tepicana* Killip. Over 800 specimens were examined in loans and visits to several herbaria, specifically ARIZ, BH, BM, BRIT, DES, FSU, GH, K, LINN, NMC, NY, PH, ROCH, UC, and US. Specimens examined are listed below, and these records, often with more collection information, have also been deposited in the archives of the botany libraries of the University of Arizona herbarium (ARIZ), L.H. Bailey Hortorium at Cornell University (BH), and the Gray Herbarium at Harvard University (GH).

Living material of *P. arida* and *P. foetida* var. *arizonica* was obtained from seed, cuttings and via fieldwork. Seed and cuttings of *P. arida* from Arizona were obtained from several individuals and academic/botanical/research institutions in the Phoenix and Tucson areas. Material of *P. foetida* var. *arizonica* was collected on a research visit to southern Arizona in late August and early September, 2001. All living material was cultivated in greenhouses at Cornell University, Harvard University and the University of Rochester.

Determinations of bedrock types in Arizona were made from Wilson et al. (1960), of soils for Santa Cruz County from Richardson et al. (1979) and of soils for southernmost Pima County from unpublished maps provided by the United States Department of Agriculture Natural Resource Conservation Service in Tucson, Arizona. Geographic localities were determined, whenever possible, using a variety of map and gazetteer references for different countries, specifically Argentina (United States Board on Geographic Names 1968), Guatemala (Defense Mapping Agency 1984; Instituto Geográfico Militar 1989), Mexico (United States Board on Geographic Names 1956; Cea-Herrera et al. 1990; McGowan 1990) and Paraguay (United States Board on Geographic Names 1957; Dirección del Servicio Geographico Militar 1990).

DISCUSSION

Passiflora arida

Passiflora arida (Mast. and Rose) Killip, Journ. Wash. Acad. Sci. 12: 256. 1922.

Passiflora foetida L. var. *arida* Mast. and Rose, Contr. U.S. Nat. Herb. 5: 182. 1899. Type: MÉXICO: Sonora, Guaymas, *J.N. Rose 1206,* 5–11 Jun 1897 (holotype US; isotypes, GH, NY). *Passiflora arida* var. *cerralbensis* Killip, Publ. Field Mus. Nat. Hist., Bot. Ser. 19: 470. 1938. Type: MÉXICO: Baja California Sur, Ceralbo Island, Ruffo's Ranch, *I.M. Johnston 4043,* 7 June 1921 (holotype US; isotypes GH, K, NY, UC). *Passiflora arida* var. *pentaschista* Killip, Publ. Field Mus. Nat. Hist., Bot. Ser. 19: 470. 1938. Type: MÉXICO: Baja California Sur, San Jose del

Cabo, *A.W. Anthony 333*, March–June 1897 (holotype US; isotype GH).

Passiflora arida is a morphologically diverse species that was recognized by Killip (1938) to contain three questionably distinct varieties, the typical variety, var. *cerralbensis* Killip and var. *pentaschista* Killip. Plants of *P. arida* in Arizona fit var. *pentaschista*. The morphological description provided below summarizes all of the variation within the species; character states defining var. *pentaschista* are enclosed in parentheses. An illustration fitting typical var. *pentaschista* is provided in Fig. 1.

Liana, rarely shrubby, stem terete, densely pubescent with short, erect to curled (erect) trichomes; leaves malodorous when bruised, very densely pubescent, often lanate on both surfaces, trichomes white, golden to red-brown, straight to curled (straight), glandular trichomes absent, or if present then rare along the leaf surfaces and petiole, particularly along the leaf margin where larger veins terminate, these trichomes greatly reduced in size, shorter than the normal trichomes and with very reduced to absent capitula; leaves ovate in general outline, entire to rarely dentate (entire to dentate), basally cordate to truncate, 2–7 (3–6) cm long by 2–8 (2–7) cm wide, with 3–9 (3–9, typically 5–7) rounded to acuminate lobes, the sinus between main central lobe and first adjacent lobe 0.5–3.7 (0.7–3.7) cm deep, the sinus between the first and second adjacent lobes 0–1.6 (0.1–1.6) cm deep, petioles 0.5–3.4 (0.6–2.8) cm long; stipules semiannular, pinnatifid to pinnatisect, pubescent, eglandular, 0.1–1.2 (0.2–1.0) cm long, with several narrow, erect segments, the largest towards the side of the stem of leaf attachment; tendrils pubescent, usually functional, to 15 cm long; peduncle 1.4–6 (1.4–3.0) cm, often elongating 1 cm or more in fruiting material; floral bracts green to red, pinnatifid, densely pubescent, eglandular (rarely with scattered, reduced glandular trichomes), branched to 3 or uncommonly 4 orders, 1.5–3.3 (1.6–2.8) cm long by 1.4–2.8 cm wide, midrib 0.5–2 mm wide, bracts enlarging significantly with fruiting and frequently persistent, becoming longer than the fruit; buds 2.0–2.5 cm long, acuminate; flowers 3–5 cm wide, lightly fragrant, usually solitary at nodes, rarely in pairs; sepals ovate-lanceolate, with a subapical, green, acicular, aristate appendage 0.3–1.0 (0.5–1.0) cm long, abaxial sepal surface greenish, moderately to strongly pubescent, particularly along main veins, adaxially white and glabrous, 1.3–2.3 cm long by 0.5–0.9 cm wide; petals white, ovate-lanceolate, glabrous, apically denticulate, 1.2–2.0 (1.4–2.0) cm long by 0.5–0.8 cm wide; corona consisting of 5–6 series of filaments, two large outer series 0.6–1.7 (1.0–1.7) cm long with the basal ⅕th purple to magenta, particularly on the upper surface, terminal half pale pink and medial portion white, and 3–4 irregular inner series of short, thin,

erect filaments 1–2 mm long, purple to magenta (color patterns presented here are based on cultivated plants fitting var. *pentaschista*); floral tube 3–5 mm deep, operculum thin, erect, 1–2 mm wide, nectar ring thicker, erect, perpendicular to the main axis of the flower, ca. 1 mm wide, limen erect, 10–20° from vertical, arising from the base of the floral tube, 2–4 mm wide, margin entire (these observations of floral tube components are based primarily on cultivated plants fitting var. *pentaschista*); androgynophore 0.4–0.8 cm long, smoothly cylindrical along its entire length and basally flared like an inverted cone, with numerous magenta longitudinal streaks and spots; stamen filaments 0.4–0.7 (0.4–0.6) cm long by 0.1–0.15 cm wide; anthers 0.4–0.6 cm long by 0.15–0.25 cm wide; ovary subglobose to ovoid, densely pubescent, 0.3–0.5 cm long, styles nearly white, pubescent adaxially, 0.3–0.9 (0.45–0.9) cm long, stigmas 0.5–2.5 (1.0–2.5) mm wide, green, emergent; fruit a berry, orbicular to ovoid (ovoid), round in cross-section, pubescent, green to yellow-green, occasionally with red, 1.5–3.0 cm long by 1.5–2.5 cm wide; seeds flattened, reticulate, narrowed basally and with three apical teeth, 3.0–5.0 (3.0–4.0) mm long by 1.5–3.0 (1.5–2.0) mm wide, enclosed in a nearly translucent, fragrant, sweet aril.

Passiflora arida sensu lato has a native range from southernmost Baja California and southernmost Sonora northward to extreme southeastern Baja California (norte) and the municipalities of Pitiquito and Trincheras in northern Sonora (Fig. 2). Reports of *P. arida* from Sinaloa (Shreve and Wiggins 1964; Wiggins 1980) are from misidentified specimens of unusually pubescent *P. foetida* var. *gossypiifolia* (e.g., *Mexia 49.5*; *Ortega 7230*; *Rose et al. 13688*; see Specimens Examined). Variety *arida* is found throughout the entire range of the species except in extreme southern Baja California and Sonora and flowers year-round, but primarily from March to May. Variety *cerralbensis* is present only in the southern half of Baja California Sur and part of coastal southern Sonora and also flowers throughout the year, but most commonly from October to February. Variety *pentaschista* grows in the southern half of Baja California Sur, particularly the extreme south, and is also found in southernmost Sonora and flowers primarily in the spring and autumn. The daily flowering time is unknown for *P. arida* sensu lato, but occurs in the early morning in var. *pentaschista*. It may be the same for the other putative varieties, and many other members of the subgenus also flower at this time of day.

The primary differences between the varieties of *P. arida* appear to be the following. In var. *arida* leaves typically have three rounded lobes, whereas in var. *cerralbensis* leaves are typically 3-lobed but occasionally 5-lobed, with round to acute apices. Leaves of var. *pentaschista* only have three lobes in young or regenerating plants and otherwise have leaves with 5, 7, or rarely 9 lobes. The largest lobes
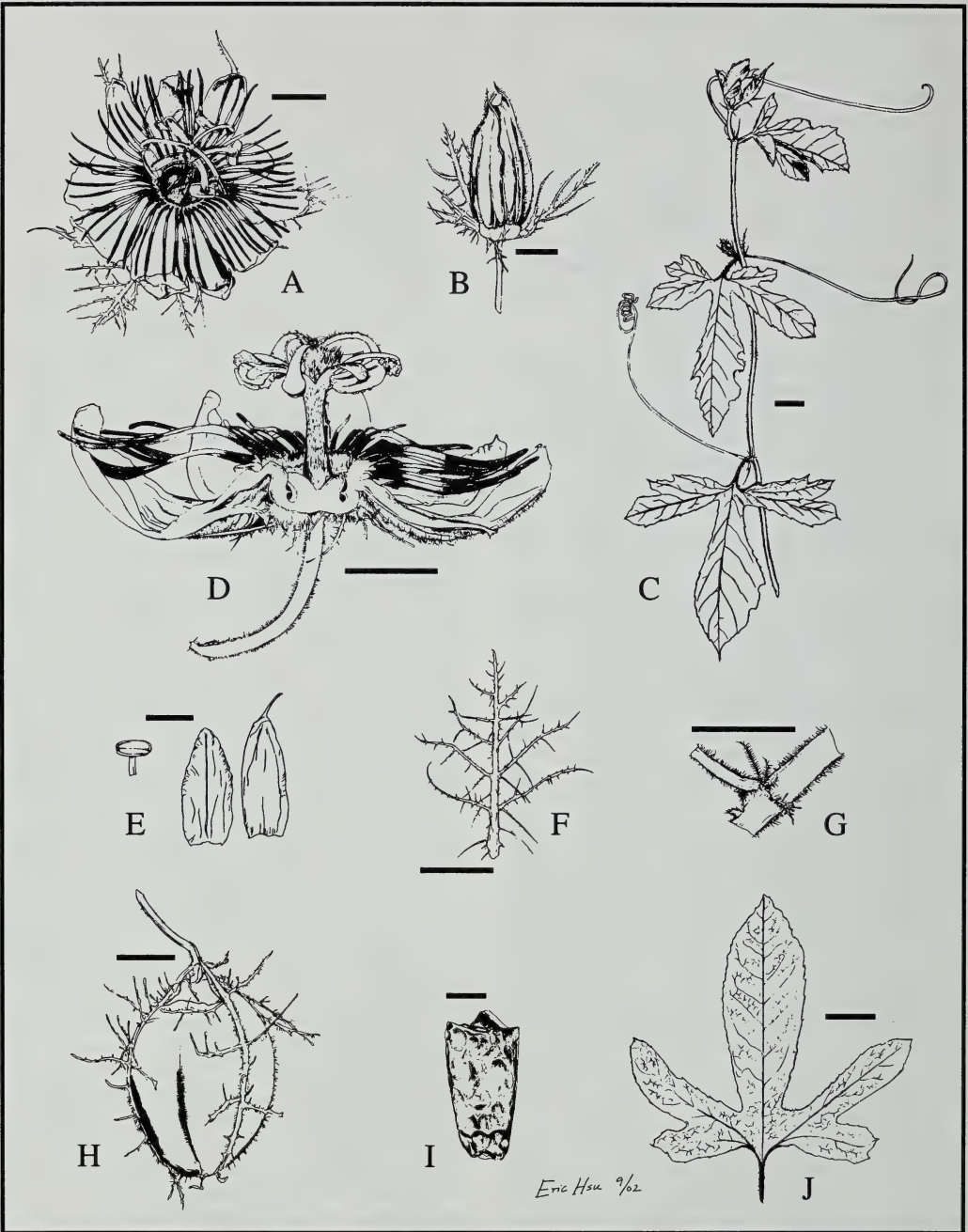
Fig. 1. *Passiflora arida.* Illustration based on plants approximating var. *pentaschista.* Scale bars all represent one centimeter, except in I where it represents one millimeter. A, flower top-view; B, flower bud; C, stem; D, flower cross-section; E, anther, petal, and sepal; F, floral bract; G, stipule; H, fruit; I, seed; J, leaf.

are typically narrowed basally, apically rounded to acute and entire to dentate. The pubescence on the leaves of var. *arida* consists of a dense layer of curled trichomes that are gray to red-brown or golden, which gives the veins on the abaxial leaf surfaces a particular physical prominence. With var. *cerralbensis* the pubescence is nearly as dense, but consists of mostly straight gray to red-brown or golden trichomes that tend to follow the direction of the dividing leaf veins. Variety *pentaschista*
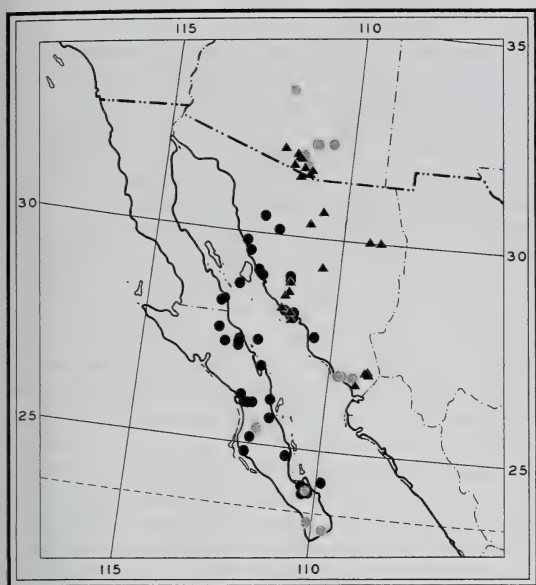
FIG. 2.   Map of the geographic ranges of *Passiflora arida* (circles) and *P. arizonica* (triangles). Gray circles represent plants approximating *P. arida* var. *pentaschista,* and black circles represent the remainder of *P. arida.*

tends to have long straight trichomes on the leaves, although those approaching the form of the other varieties can occur and are typically gray, rarely red-brown. Floral bracts and stipules are smallest, most compact and most densely pubescent in var. *arida* and least so in var. *pentaschista.* Furthermore, the glandular trichomes typical of the subgenus are essentially absent in var. *arida,* and present but greatly reduced and uncommon in var. *pentaschista,* the glandular apex of such trichomes also extremely reduced. Glandular trichomes in var. *cerralbensis* tend to be morphologically intermediate to those of the other two varieties.

Specimens morphologically intermediate between the varieties, however, are not uncommon and one variety seems to flow into another. For example, in leaf shape most specimens of var. *cerralbensis* are not exactly like the type specimen of this variety (*Johnston 4043*), this collection with leaves approaching (at GH, NY, UC, US), or essentially identical (at K) in shape to most plants of var. *pentaschista.* None of the varieties can be clearly circumscribed based on their current definitions, and for that reason I do not recognize them as being distinct from one another. However, for the convenience of the reader, in this manuscript I indicate which specimens most closely approximate the type of var. *pentaschista,* as it is this morphological phase of the species that occurs in Arizona. Further taxonomic evaluation within this species is necessary.

Passiflora arida *in Arizona.* On 17 August 1999, Spellenberg and Zucker (*12959*) collected what was

thought to be *P. foetida* var. *arizonica* in Gates Pass, near Tucson, Arizona (see Specimens Examined section). Soon after, examination by John MacDougal at the Missouri Botanical Garden determined that this specimen was one of *P. arida.* This appears to have been the first collection of *P. arida* made from the United States. Complementary to the observation of this specimen, I noted that the material I received of *P. foetida* var. *arizonica* was instead *P. arida,* this material from Reddington Pass near Tucson, Las Guijas Mountains near Tucson, Tohono Chul Park near Tucson (their source being the Coyote Mountains near Tucson), the Arizona-Sonora Desert Museum near Tucson, and the Desert Botanical Garden near Phoenix (also see Specimens Examined section). Furthermore, living material of *P. arida* was obtained from the teaching greenhouse at the University of Connecticut, Storrs, was also misidentified as *P. foetida* var. *arizonica.* This material was obtained by University of Connecticut in 1999 as seed with this identity from the Passiflora Society International by a University of Connecticut employee, John Maugeri.

In addition, during an internet search for *Passiflora* in Arizona, an e-mail was found on the Arizona Native Plants list server mentioning an adventive *P. foetida* (http://listserv.arizona.edu/cgi-bin/wa?A2=ind9610&L=azplants&P=R339). This message, posted on 22 October 1996 by Katherine Waser of the Office of Arid Lands Studies at the University of Arizona, contained a statement that "some kind and considerate birds planted seeds of *Passiflora foetida* under my orange tree." Suspecting that this could be *P. arida,* I contacted Katherine Waser to obtain some material from this plant to confirm its identification. The material that was sent was indeed *P. arida,* which has persisted on her property since 1996, probably by seed regeneration.

Sources of material sent to me from Arizona were typically from true desert habitat around Tucson, although it has been found in dry oak savanna and grassland at higher elevations (e.g., the Coyote Mountains), as well as in cultivated areas that may receive some supplementary water, indicating a diversity of habitat tolerance. In the true desert areas the plants may occur in somewhat disturbed locations with available water run-off. For instance, in Gates Pass to the west of Tucson it grows in such a site beside a parking lot and at the base of a hill with *Machaeranthera tanacetifolia, Carnegiea gigantea, Larrea tridentata, Simmondsia chinensis, Prosopis velutina* and *Fouquieria splendens.*

Passiflora arida probably first appeared in the United States by the late 1980s. Seed supplied to me in 2001 by the Desert Botanical Garden's seed storage facility was originally obtained in October 1987, in Las Guijas Mountains near Tucson, identified as *P. foetida* var. *arizonica.* Only one seed germinated, but it gave rise to a plant that is *P. arida,* making this very young plant the first record

of the species in the U.S., because the seed from which it came was over thirteen years old (see Specimens Examined). Furthermore, a published photo exists of *P. arida* cultivated at the Desert Botanical Garden in 1988, although it was also misidentified as *P. foetida* var. *arizonica* (see Hodgson 2001).

Plants approximating the type of *P. arida* var. *pentaschista* have been collected in Sonora only since 1988 (*Jenkins et al. 88-98*; *Sanders et al. 9254*; *Van Devender et al. 93-950*; see Specimens Examined), and in a small region relatively close to Huatabampo. Previously, this taxon had been assumed to be endemic to southern Baja California Sur (Wiggins 1980). Whether this represents a recent introduction to southern Sonora, or native populations in a small region that has been floristically undersampled, is not clear, although natural floristic disjunctions between Baja California and Sonora are known to occur (see Shreve and Wiggins 1964; Felger and Lowe 1976). Yet, whether *P. arida* originally arrived in Arizona via natural or anthropogenic dispersal northward from Baja California or Sonora remains a mystery.

Within Arizona, *Passiflora arida* would have been misidentified as *P. foetida* var. *arizonica* because there are no other members of the subgenus in Arizona, and due to the morphological distinctiveness of the subgenus it could only be best identified with local taxonomic keys and descriptions (see Kearney and Peebles 1942, 1951; Tidestrom and Kittell 1941) as the latter species. However, this error has apparently become cumulative, as material cultivated around the world identified as *P. foetida* var. *arizonica* is likely *P. arida*. Such is the case with material obtained from the University of Connecticut (see Specimens Examined). A discussion of the distinction between these taxa is given below under *P. arizonica*.

Although unlikely, *P. arida* could be misidentified in Arizona as *P. bryonioides,* a relatively unrelated species (subgenus *Decaloba* (DC.) Reichb., section *Pseudodysosmia* (Harms) Killip), based on similar leaf shape. However, *P. bryonioides* has green leaves with erect glands on the petioles, undivided semi-annular stipules, small linear-lanceolate floral bracts, scabrous pubescence of hooked trichomes over all vegetative parts of the plant, and glabrous green fruit shaped like a football (American). *Passiflora arida* has gray-green leaves without glands on the petioles, deeply divided stipules, large pinnatifid floral bracts, a soft whitish nonhooked pubescence over all vegetative parts, and a pubescent ovoid fruit.

Potential invasiveness. An important issue to address with this species, at least in what has been recognized as var. *pentaschista,* is its potential threat as a weed. It clearly has shown its ability to spread in desert areas in portions of southern Arizona, which would suggest both drought tolerance

and successful seed dispersal. The seeds are probably spread by birds and small mammals (MacDougal 1994). Although it is native to desert and semi-desert areas in southern Baja California (Wiggins 1980) and Sonora, in cultivation it shows little tolerance for drought, suggesting it has very deep roots where growing in deserts. Furthermore, in cultivation it displays abundant, rapid and smothering growth in humid, frequently-watered conditions, suggesting that it would do very well in climates providing such conditions. However, plants cultivated outdoors in Rochester, New York, have survived frosts and mild freezes, which is probably also the case for naturalized plants in southern Arizona. Mature plants in such greenhouse conditions also tend to flower frequently and set fruit in great abundance apparently without pollinator visitation. Thousands of seeds can be produced by a healthy plant within a few months, the majority of which germinate rapidly. Even so, considerable seed dormancy is evident and seeds several months to a year old have germinated with little difficulty at Cornell University and the University of Rochester, and can be viable over even longer periods, as is evident from the thirteen-year-old seed germinated from the Desert Botanical Garden. Seeds probably can tolerate periods of freezing as well. Considering these factors, it seems possible that this species could potentially be a problematic invasive if introduced into more southern latitudes in the United States, or anywhere with some moisture and significant warmth.

Passiflora arida is a relatively localized endemic, found only in portions of the Sonoran Desert, and in the case of the so-called var. *pentaschista* is found restricted to southern Baja California and extreme southern Sonora. Yet this would not be the first locally restricted plant species to rampage once removed from its relatively small home range. *Robinia pseudoacacia,* probably native only to portions of the Appalachian and Ozark Mountains in the eastern United States, has shown substantial invasive ability where introduced throughout the northern temperate zone (Fernald 1950; Hunter 2000). And the relatively more restricted endemic, *Lupinus arboreus* Sims, native to a limited number of coastal counties in California, has been spread anthropogenically for horticulture and dune stabilization. This species has also spread abundantly by natural means since then, and now can be found along the Pacific coast north to British Columbia, occasionally occupying inland sites (Pickart 2000). The issue of plant invasiveness is becoming more openly discussed in recent years and a greater effort is being made to evaluate this problem (see Baskin 2002; Board on Agriculture and Natural Resources and Board on Life Sciences 2002; Reichard and Hamilton, 1997; also see http://www.mobot.org/iss). Other members of *Passiflora* have exhibited the ability to naturalize (Smith 1976; Webb et al. 1988; Hrusa et al. 2002), especially the notorious

P. tarminiana Coppens and V.E.Barney (d'Ecken-brugge et al. 2001; previously considered to be *P. mollissima* [Kunth] Bailey), an aggressive weed in Hawaii (La Rosa 1984) and New Zealand (Webb et al. 1988). Perhaps *Passiflora arida* has the potential to follow this pattern of invasiveness, and caution should be exercised by horticulturists and plant enthusiasts because of the international distribution of seed. Further evaluation of the invasive potential of this species is necessary.

Passiflora arizonica

Passiflora arizonica (Killip) D.H. Goldman comb. nov.—Type: USA, Arizona, Pima County, Fresnal Canyon, Baboquivari Mts., *G.J. Harrison 4774*, 26 September 1927 (holotype, US). *Passiflora foetida* var. *arizonica* Killip. Publ. Field Mus. Nat. Hist., Bot. Ser. 19: 490. 1938.

Liana, occasionally a climbing, spreading, low shrub with numerous short, leafy branches, stems terete, pubescent with short, erect, white to gray trichomes; leaves malodorous when bruised, densely pubescent, villous, with erect, white to rarely red-brown trichomes and numerous elongate capitate glandular trichomes, glandular trichomes abundant along both leaf surfaces, petioles and particularly the leaf margins; leaves ovate in general outline, frequently coarsely dentate, basally cordate, 1.5–5 cm long by 1.0–7.0 cm wide, with 3–5 lanceolate, acuminate lobes, the sinus between the main central lobe and the first adjacent lobe 0.2–2.5 cm deep, the sinus between the first and second adjacent lobes 0.0–0.6 cm deep, petioles 0.2–4.0 cm long; stipules glandular-viscid, semi-annular, pinnatifid, 0.1–0.8 cm long, with several narrow, erect segments, the largest towards the side of the stem of leaf attachment; tendrils pubescent, frequently functional, to 16 cm long, but often small and non-functional; peduncle 1.7–6.5 cm long, frequently elongating a centimeter or more in fruit; floral bracts green to red, pinnatifid, pubescent, very glandular-viscid with numerous capitate glandular trichomes, branched to 2 or uncommonly 3 orders, 1.5–3.5 cm long by 1.0–2.8 cm wide, midrib 1.0–2.5 mm wide, bracts often enlarging in fruit but not always persistent, often shorter than the fruit; buds 2.5–3.5 cm long, acuminate to acute; flowers 4.0–6.5 cm wide, strongly fragrant, usually solitary at nodes, rarely in pairs; sepals ovate-lanceolate, with a subapical, green acicular aristate appendage 0.3–0.5 cm long, abaxial sepal surface pale green and moderately pubescent, particularly along main veins, but often whitened at the margins and with red along the veins, adaxially white and glabrous, 1.7–3.8 cm long by 0.6–0.9 cm wide; petals white, obovate-lanceolate to ovate-lanceolate, entire, 1.6–3.0 cm long by 0.6–1.2 cm wide; corona consisting of 5–6 series of filaments, the two large outer series 0.9–2.5 cm long with the basal half white, particularly on the upper surface, the apical

half pale purple, the 3–4 irregular inner series of short, thin, erect filaments around 2 mm long, basally white and apically pale purple to pale magenta; floral tube 5–7 mm deep, operculum thin, erect, around 2 mm wide, nectar ring thicker, erect, at about 45° to the main axis of the flower, around 2 mm wide; limen erect, around 45° from vertical, arising from the base of the androgynophore 1–2 mm above the base of the floral tube, 3–4 mm wide, margin entire, flared outward; androgynophore 0.7–1.2 cm long, basally expanded into a widened cylinder or inverted cup and slightly expanded again just below the point of stamen filament divergence, the basally expanded region white, with several small magenta spots occurring in the narrower portions above and rarely extending to the base; stamen filaments 0.5–1.0 cm long by 0.1–0.2 cm wide; anthers 0.6–0.9 cm long by 0.2–0.4 cm wide; ovary globose, densely pubescent, 0.3–0.5 cm long, styles white, pubescent and often with purple spotting adaxially, 0.7–1.4 cm long, stigmas 1.0–2.5 mm wide, green, emergent; fruit a berry, ovoid to basally and/or apically truncate, triangular to round in cross-section, pubescent, green to yellow-green, 2.0–3.5 cm long by 1.8–3.0 cm wide; seeds flattened, reticulate, narrowed basally and with three apical teeth, 5.0–7.0 mm long by 2.5–4.0 mm wide, enclosed in a nearly opaque, whitened, fragrant, bittersweet to sour aril. See Fig. 3 for illustration.

This species is here elevated from varietal rank based on its particular distinctiveness in floral morphology and phenology. Restricted to portions of Pima and Santa Cruz Counties in Arizona and several municipalities in eastern Sonora, Mexico (Fig. 2), *P. arizonica* grows from near sea level to 1800 m, typically from 1000–1800 m in Arizona where it is primarily just beyond the typically defined boundaries of the Sonoran Desert (see Shreve 1942; Shreve and Wiggins 1964). Flowering primarily from May through December, most flowering occurs in August and September, during the summer monsoon season. Unlike most members of the genus, particularly the subgenus *Dysosmia* (see Janzen 1968, for discussion of *P. foetida*), *P. arizonica* flowers in the evening, with flowers typically opening around 4–5 p.m. and closing around midnight. This fact is only recorded by Kearney and Peebles (1951), and in a specimen by Peebles (*8806* [US]) both of which state that the flowers are apparently "vespertine." This feature, plus the light color of the flowers, the pleasant fragrance noticeable from some distance, and the relatively deep floral tube suggest moths as pollinators. Members of Noctuidae and some Sphingidae are known nocturnal visitors of flowers, and the former are known to travel upwind at times of feeding, putatively locating flowers by scent (see Proctor et al. 1996, for a review).

Based on field observations made with my collections *2109* and *2120* (see Specimens Examined),
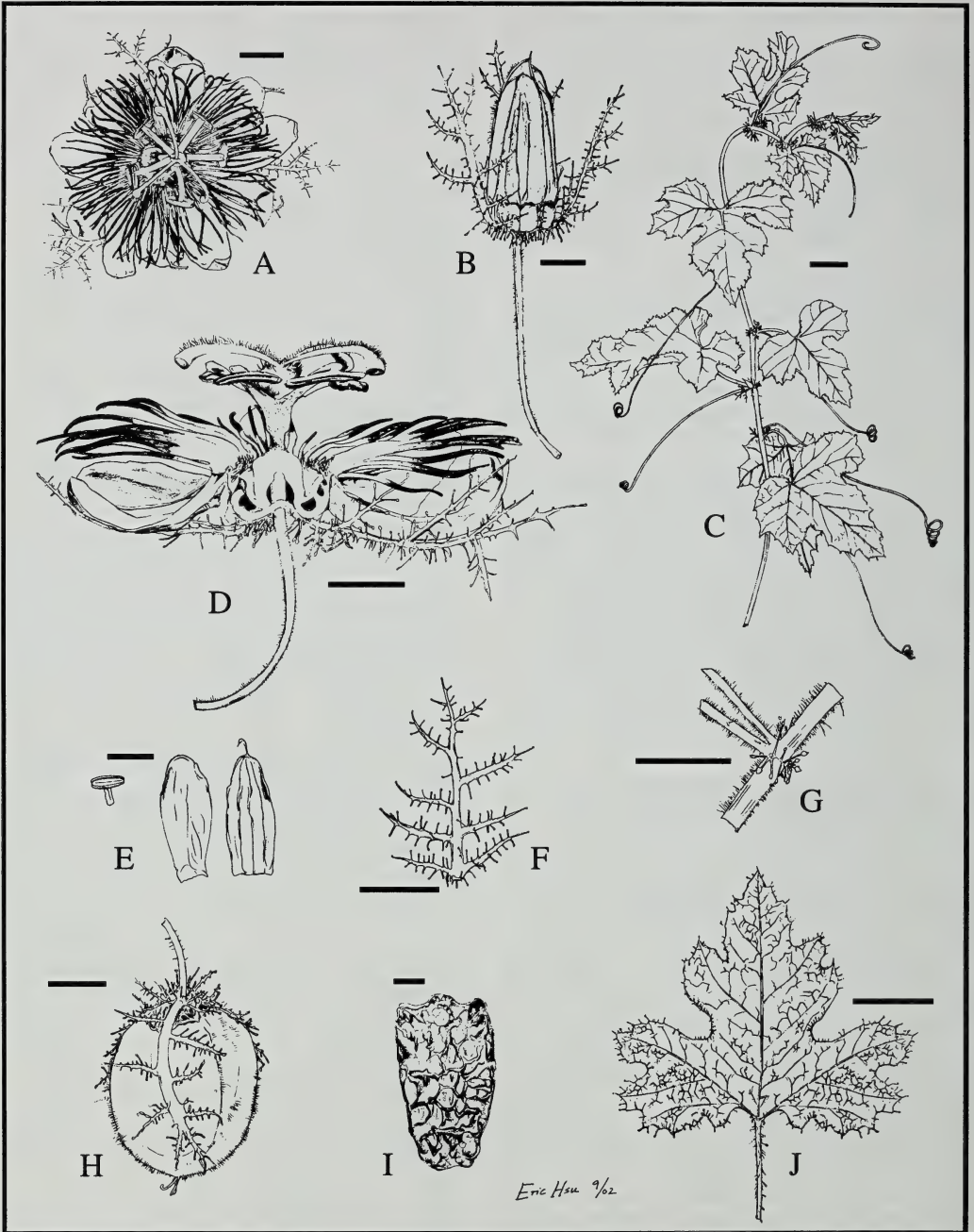
Fig. 3. *Passiflora arizonica.* Scale bars all represent one centimeter, except in I where it represents one millimeter. A, flower top-view; B, flower bud; C, stem; D, flower cross-section; E, anther, petal, and sepal; F, floral bract; G, +stipule; H, fruit; I, seed; J, leaf.

at least in portions of southern Arizona this species seems to prefer south to west-facing exposures on granite or related igneous rock. Where collected in the southern portion of Coronado National forest (*2109*), in the vicinity was granite, diorite, Meso-

zoic andesite or rhyolite and possibly Cretaceous-tertiary porphyry and granite. Soils were of the steep Lampshire-Chiricahua association (Lithic Ha-plustolls and Ustollic Haplargids, respectively), which are mollisols and aridisols that are derived

TABLE 1. COMPARISON OF FEATURES USED TO DISTINGUISH *PASSIFLORA ARIDA* (≈VAR. *PENTASCHISTA*) FROM *P. ARIZONICA*.

Character	Passiflora arida	Passiflora arizonica
Glandular trichomes on leaves, stipules, and involucral bracts	No, or small and inconspicuous	Yes, obvious
Number of lateral leaf lobes	2–8	2–4
Sinus depth between apical lobe and main side lobes	0.7–3.7 cm	0.2–2.5 cm
Sinus depth between largest and 2 largest side lobes	0.1–1.6 cm	0.0–0.6 cm
Petiole length	0.6–2.8 cm	0.2–4.0 cm
Peduncle length (at flowering)	1.4–3.0 cm	1.7–6.5 cm
Involucral bract branching orders	3 (–4)	2 (–3)
Involucral bract lengths	1.6–2.8 cm	1.5–3.5 cm
Sepal length	1.3–2.3 cm	1.7–3.8 cm
Petals	1.4–2.0 cm × 0.5–0.8 cm	1.6–3.0 cm × 0.6–1.2 cm
Corona filament length, outer two series	1.0–1.7 cm	0.9–2.5 cm
Color pattern of large coronal filaments	Basal fifth magenta, apical half purple, white between	Basal half white, apical half purple
Androgynophore length	0.4–0.8 cm	0.7–1.2 cm
Androgynophore basal shape	Inverted cone	Inverted cup
Stamen filament length	0.4–0.6 cm	0.5–1.0 cm
Anthers	0.4–0.6 cm × 0.15–0.25 cm	0.6–0.9 cm × 0.2–0.4 cm
Style length	0.45–0.9 cm	0.7–1.4 cm
Seeds	0.3–0.4 cm × 0.15–0.2 cm	0.5–0.7 cm × 0.25–0.4 cm
Daily flowering time	Early morning	Evening, dusk
Floral fragrance	Weak to moderate	Strong

from igneous rock. In southern Pima County (Buenos Aires National Wildlife Refuge; *2120*) the bedrock was Cretaceous-tertiary granite, with the associated soil type as Lampshire-Romero-rock outcrop complex, with Romero soils perhaps similar to those of the Chiricahua series and also derived from similar bedrock types. In Buenos Aires National Wildlife Refuge this species has previously been observed in canyons and on rocky slopes (McLaughlin 1990).

In Coronado National Forest (Santa Cruz County) I found *P. arizonica* growing at about 1200 m with *Carnegiea gigantea* (rare), *Celtis pallida*, *Chenopodium watsoni*, *Dodonea viscosa*, *Eriogonum wrightii*, *Erythrina flabelliformis*, *Eupatorium solidaginifolium*, *Eyesenhardtia polystachya*, *Fouquieria splendens*, *Gomphrena sonorae*, *Jatropha cardiophylla*, *Mimosa dysocarpa*, *Plumbago scandens*, *Quercus emoryi*, and *Waltheria americana*. In Buenos Aires National Wildlife Refuge (southern Pima County) I observed it growing at about 1100 m with *Artemesia* sp., *Astrolepis sinuata*, *Bouteloua repens*, *Boerhaavia purpurascens*, *Cheilanthes wootoni*, *C. wrightii*, *Dalea* sp., *Dasylirion wheeleri*, *Eragrostis lehmanniana*, *Eriogonum* sp., *Eyesenhardtia polystachya*, *Fouquieria splendens*, *Heteropogon contortus*, *Iva xanthifolia*, *Janusia gracilis*, *Manihot angustiloba*, *Mimosa dysocarpa*, *Notholoaena grayi*, *Prosopis velutina*, *Quercus oblongifolia*, *Stipa* sp. and *Talinum paniculatum*. At both sites there were potentially very old plants of *Passiflora arizonica*, with gnarled, woody stems in excess of 3 cm in

diameter at soil-level. In comparison, much more vigorous and rapidly growing 2 year-old plants at Cornell and Harvard have stems less than 0.5 cm in diameter at soil-level.

Comparison to similar species. Passiflora arizonica is easy to distinguish from *P. arida* (Table 1). *Passiflora arida* lacks the obvious glandular trichomes that are so abundant in *P. arizonica*, and generally has more numerous, longer and narrower leaf lobes than *P. arizonica*. The leaves of *P. arizonica* resemble those of many species of *Acer*, whereas the leaves of *P. arida* do not. The petioles of *P. arida* are also usually much shorter than those on *P. arizonica*. Peduncle length can be considerably shorter in *P. arida* than in *P. arizonica*, although not always. Floral bracts are divided to three, rarely four orders in *P. arida*, whereas only to two or rarely three orders in *P. arizonica*, and the floral bracts of the latter can be longer than the former at flowering. Sepals and petals tend to be smaller in *P. arida* than *P. arizonica* and the outer two series of coronal filaments tend to be shorter as well. The color pattern on these coronal filaments is distinct, in *P. arida* the basal ⅕th purple to magenta (particularly the upper surface of the filaments), the apical half pale pink above and below, and the medial portion white. The outer two series of coronal filaments of *P. arizonica* are pale purple in the apical half, particularly along the bottom surface, and white in the basal half, more so to the top. *Passiflora arizonica* can have a longer

androgynophore than *P. arida* and the shape of the basal portion is an expanded cylinder or inverted cup (reminiscent of *P. edulis*), whereas it is more of a flared base or inverted cone (typical for the subgenus) in *P. arida*. The stamen filaments can be longer in *P. arizonica* than in *P. arida*, and the anthers are much larger in the former compared to the latter. The style length of *P. arida* is generally much shorter than that of *P. arizonica* and the seeds of *P. arida* are always smaller than those of *P. arizonica*. The two species are isolated reproductively as *P. arida* flowers early in the morning with relatively little floral fragrance and *P. arizonica* flowers in the evening with a strong fragrance. Furthermore, the seed of *P. arida* tends to germinate rapidly, whereas seed of *P. arizonica* express strong dormancy, which seem to have to go through several cycles of heat, moisture and dryness before germination occurs, although the exact germination trigger in this species is yet unclear. Extended periods of heat have been inferred to break dormancy in seeds of other *Passiflora* species (Williams and Buxton 1995). Currently these two species occupy different habitats, at least in Arizona, although this may change as *P. arida* continues to increase its range.

Although unlikely to be mistaken for *P. arizonica*, *P. fruticosa* from southern Baja California and *P. palmeri* var. *palmeri* from much of Baja California and some islands in the Gulf of California (Felger and Lowe 1976) are likewise dryland plants in the subgenus *Dysosmia*. These shrubby species are not sympatric with *P. arizonica*, but are with *P. arida*. Both of these Baja endemics or near-endemics have non-functioning tendrils and frequently form relatively short, densely leafy branches, an occasional feature in *P. arizonica* and some *P. arida*. Both species almost always have three-lobed leaves like typical *P. arida* and lack the dentations of *P. arizonica*. However, like *P. arizonica* and unlike *P. arida* the floral bracts are extremely glandular, particularly in *P. fruticosa*. The leaves of *P. fruticosa* are fringed with very short glandular trichomes less than 5 mm long and not obvious, whereas *P. palmeri* has much larger glandular trichomes along the leaf margins. Otherwise the plants are covered with dense, woolly pubescence reminiscent of *P. arida*. The flowers of *P. palmeri* are striking, quite large with a very long, narrow androgynophore, greatly reduced coronal filaments and linear white petals and sepals. Apparently it flowers in the morning in its very dry habitat (Rose 1892). Good photographs of these flowers exist in a book on Baja vegetation by Roberts (1989), as well as on a specimen at US (*Collins et al. 234*; see Specimens Examined). Daily flowering time is apparently unknown for *P. fruticosa*, and this species has relatively small flowers with sepals that are strongly pubescent abaxially, and otherwise has more normally proportioned flower parts like much of the subgenus as compared to *P. palmeri*.

Killip (1938) stated that *P. foetida* var. *arizonica* is most closely related to var. *vitacea* from South America, this variety included within *P. chrysophylla* by Deginani (2001). Killip also mentions in the discussion of var. *vitacea* that some specimens identified as the typical variety or the South American var. *nigelliflora* may actually be var. *vitacea*. He also states that var. *oaxacana*, native to southern Mexico, is similar overall to var. *arizonica*, is similar in leaf shape to var. *hibiscifolia* and in pubescence to var. *nigelliflora*. Variety *nigelliflora* is suggested to have a close relationship to var. *gossypiifolia* in addition to var. *vitacea*. *Passiflora foetida* var. *santiagana*, native to eastern Cuba, is placed near var. *arizonica* by Killip (1938), and was recognized as a distinct species by Borhidi and Muñiz (1971). The common features between all these taxa are a pubescent ovary and the very rare (var. *gossypiifolia*) to frequent presence of five leaf lobes.

Upon examination of specimens, in Mexico var. *oaxacana* does appear most similar overall to *P. arizonica* when compared to other regional taxa in the subgenus. But compared to those taxa that are native in closer geographic proximity, and bear putatively closer phylogenetic relationships to *P. arizonica* according to Killip (1938), specifically *P. foetida* var. *gossypiifolia* (here including the relatively indistinct *P. foetida* var. *longipedunculata*), var. *oaxacana* and *P. santiagana*, the differences from *P. arizonica* are obvious. The leaves of the other taxa never have sharp lobes, except occasionally var. *gossypiifolia*, and all but var. *gossypiifolia* frequently have five-lobed leaves. The leaf lobes of var. *oaxacana* are relatively shallow, whereas those of *P. santiagana* are shallow to deep and the leaves of both of these varieties are often smaller than those of *P. arizonica*, particularly in *P. santiagana*. Leaves of var. *gossypiifolia* can be as large as those of *P. arizonica* where their geographic ranges overlap, or even larger elsewhere and also can approach the concentration of glandular trichomes that are found on the leaves and stipules of *P. arizonica*, although the trichomes in var. *gossypiifolia* are often smaller. Such trichomes are much reduced in stature and less common, although still present, in var. *oaxacana* and *P. santiagana*. Non-glandular trichomes in these three varieties occur densely, particularly in var. *oaxacana* and *P. santiagana*, the trichomes of the latter being very short, similar to those on the abaxial leaf surfaces of var. *lanuginosa*. Stems of all these taxa are pubescent, although curiously some plants of *P. santiagana* have completely glabrous stems. The most densely pubescent specimens of var. *gossypiifolia* come from northwestern Mexico, particularly Sonora and Baja California. Plants of *P. arizonica* rarely express the density of leaf pubescence seen in these other three varieties, or more precisely with var. *gossypiifolia* in the geographic range where they both co-occur. The flowers of var. *gossypiifolia* can be of similar

size to those of *P. arizonica,* but are often smaller and have a denser ring of short coronal filaments in generally four series. The large outer two coronal series in var. *gossypiifolia* tend to be purple on the upper surface, with a gradual lightening towards the base and underside of the filaments. Furthermore, the floral tube of var. *gossypiifolia* is not as deep and has a smaller nectar ring than in *P. arizonica,* and has a flared base to the androgynophore as opposed to a large cylindrical swelling as in *P. arizonica.* Variety *oaxacana* and *P. santiagana* have much smaller flowers than *P. arizonica,* and a cylindrical base of the androgynophore has not been observed in pressed material, and if present it is quite short. The fruit in vars. *gossypiifolia* and *oaxacana,* and *P. santiagana* are smaller than in *P. arizonica,* and is largest in var. *gossypiifolia* versus var. *oaxacana* and *P. santiagana.* Furthermore, the seed of these three varieties is much smaller than that of *P. arizonica,* often around the size of *P. arida.* Flowers of var. *gossypiifolia* open in the morning unlike the flowers of *P. arizonica*; the flowering time of the other two varieties is not reported in the literature, although var. *oaxacana* has been observed to be morning-flowering (MacDougal personal communication).

Passiflora foetida var. *gossypiifolia* is probably the most widespread member of the subgenus in the new world according to Killip (1938). Distributed from Baja California, Texas and the West Indies into southern South America, it therefore could be expected to be closely involved in the biology and phylogenetic history of many other members of the subgenus. Hybridization of this variety with other *Dysosmia* taxa would not be surprising, and many specimens which could be potential hybrids with var. *gossypiifolia* have been observed in this survey. How this variety might be able to cross with a night-flowering species like *P. arizonica* is unknown, but most specimens examined of var. *gossypiifolia* from Mexico in the vicinity of Batopilas, Chihuahua, seem florally intermediate between var. *gossypiifolia* and *P. arizonica.* However, a basal cylindrical swelling in the androgynophore was not evident, and whether plants from this area are actually hybrids or a yet undescribed taxon remains unclear.

However, an unusual specimen of var. *gossypiifolia* from Guatemala (*Garcia et al. 1368*; see Specimens Examined) has many features in common with *P. arizonica.* Apparently from thorn forest near the town of Zacapa, the leaves of this specimen are five-lobed, although the two lesser lobes are much more reduced and the middle lobe more triangular and less lobed than in *P. arizonica.* This plant also appears slightly more hairy and less glandular-pubescent than most *P. arizonica.* However, flowers on this specimen appears to have a basal cylindrical swelling on the androgynophore like *P. arizonica,* but proportionally much shorter than the same structure in that species. Thus this specimen

appears to be intermediate in many respects between both *P. arizonica* and *P. foetida* var. *gossypiifolia,* and is yet not quite like either of them. Standley and Williams (1961) unfortunately make no mention of regional or unusual variation in var. *gossypiifolia* in Guatemala. Nonetheless, this specimen in conjunction with var. *oaxacana* and *P. arizonica* may represent a series of closely related taxa in Central America and to the Pacific side of Mexico.

Both *P. foetida* var. *hibiscifolia,* from southern Mexico and Nicaragua and var. *subpalmata,* also from southern Mexico, can have five-lobed leaves, especially the former. Yet Killip (1938) did not place them close to var. *arizonica* because they did not possess pubescent ovaries. Variety *hibiscifolia* typically has leaves much larger than those of *P. arizonica,* and which are entirely glabrous, as are the plants overall, similar to *P. ciliata* Aiton. Variety *subpalmata* is somewhat variable and commonly has three-lobed or five lobed leaves, with rounded lobes that can be entire to ciliate, although apparently not on the same plant. The leaves have very fine, short pubescence typically on both surfaces, and the rest of the plant is glabrous. Yet these two varieties, other than in the superficial resemblance in leaf shape, are different from *P. arizonica.* They are also probably closely related to *P. ciliata,* perhaps better included within it (MacDougal personal communication), and all have red fruit, unlike the green fruit of *P. arizonica.*

It should also be noted that all other taxa examined, those that were stated not to be of potentially close phylogenetic relationship to *P. arizonica* (see materials and methods), were very distinct from this species. These other taxa typically have three-lobed leaves that do not at all resemble the leaf features of *P. arizonica* in margins, overall outline, or type of pubescence, glandular or simple.

Specimens of variety *vitacea,* and for that matter *P. chrysophylla,* can resemble *P. arizonica* in general leaf shape, particularly the former taxon in the general outline of the leaves, both *P. arizonica* and *P. foetida* var. *vitacea* having dentate margins, but more so in the latter taxon. However, the pubescence is different in *P. arizonica* versus the other two, with *P. chrysophylla* and *P. foetida* var. *vitacea* having glandular trichomes of reduced stature, unlike the much larger ones in *P. arizonica.* Furthermore the stipules lack the degree of glandularity found in *P. arizonica,* are large with a relatively broad main segment in *P. foetida* var. *vitacea* and are greatly reduced in size in *P. chrysophylla.* The floral bracts of *P. chrysophylla* are also greatly reduced, being once-pinnatifid to simple, although in *P. foetida* var. *vitacea* they are of more typical form for the subgenus. Finally, the sepals of these South American taxa tend to be strongly abaxially pubescent and glandular-punctate, often less so in *P. chrysophylla* (this does not exactly follow Killip [1938]). The abaxial sepal surfaces of *P. arizonica*

are less pubescent than in the other taxa and are not glandular-punctate. There is an abundance of specimens of these South American taxa that are intermediate to each other, blurring the circumscriptional boundary between them, and elements of *P. arizonica* are reflected in many of these uncertain specimens and of "true" *P. chrysophylla* or *P. foetida* var. *vitacea,* although no specimen seen of these two taxa or their intermediates strongly resembles *P. arizonica.*

However, unlike all of the previous taxa examined, numerous specimens of *P. foetida* var. *nigelliflora* are nearly identical vegetatively to *P. arizonica,* particularly in leaf morphology, some of which is evident in the original description and accompanying illustration (Hooker 1839). Leaf shape of most specimens is three to five-lobed with serrate margins and numerous and large glandular trichomes. Nonglandular pubescence on the leaves ranges from dense in some specimens to more sparse, but still at the apparent density found in most specimens of *P. arizonica.* There is even some potential floral similarity, with a possible unusual swelling at the base of the androgynophore, although this is not particularly obvious in dried material. Furthermore, label data from one specimen from Argentina (*King 611;* see Specimens Examined) states "flowers striking, white with violet streaks," which sound similar in appearance to *P. arizonica.* Variety *nigelliflora* also flowers at the opposite time of the year, during the South American summer, as *P. arizonica* and can also grow in dry habitats (along with *P. chrysophylla* and *P. foetida* var. *vitacea*). The time of day that var. *nigelliflora* flowers was not determined in this survey. Although var. *nigelliflora* may be the South American counterpart to *P. arizonica,* there are several clear differences. The stipules on var. *nigelliflora* are very large, up to 2 cm long, a great deal larger than those in *P. arizonica.* Furthermore the flowers of *P. nigelliflora* are considerably smaller than those of *P. arizonica,* as are the fruit and seeds. And the androgynophore swelling, if indeed present, is proportionally shorter relative to entire androgynophore length than that in *P. arizonica.* Furthermore, var. *nigelliflora* has a very large range, from northern Argentina and Paraguay to southern Brazil (see Cervi 1990) and Uruguay, and appears to introgress with var. *vitacea, P. chrysophylla* and perhaps several other taxa throughout the region. It is quite polymorphic and was not recognized as distinct from the typical variety of the species by Deginani (2001), and Killip (1938) also puzzled over the considerable morphological flexibility in var. *nigelliflora.* Furthermore, no specimen was seen at Kew which, based on limited label data, clearly matched that described in the protologue for *P. nigelliflora* Hook. (Bot. Mag. 65: t. 3635. 1839) and lectotypification may be necessary. This taxon is in need of further investigation.

If *P. arizonica* is indeed very closely related to *P. foetida* var. *nigelliflora* then this would follow a specific biogeographic pattern of taxonomic disjunction and close phylogenetic relationships between North and South American deserts, a pattern as yet not clearly identified in *Passiflora.* Numerous examples of this pattern have been documented for other families, for example Apiaceae (Constance 1963), Asteraceae (Chambers 1963; Ornduff 1963), Hydrophyllaceae (Heckard 1963) and Zygophyllaceae, most notably in the genus *Larrea* (Hunziker et al. 1972, 1977). An extensive list of disjunct or related taxa following this biogeographic pattern is presented in Raven (1963). The deserts of North and South America have also been noted to be similar in many precise climatological and plant morphological features, particularly between the Sonoran Desert and the Monte of Argentina (Solbrig 1972). Thus it is not surprising that a taxonomic connection may exist between *Passiflora* species from these two regions, but this issue requires much more study. This should help to emphasize the need to better understand the morphology and circumscription of *P. foetida* var. *nigelliflora,* as well as all of *P. foetida* sensu lato and the subgenus *Dysosmia* as a whole.

SPECIMENS EXAMINED

Passiflora arida

Collections marked by an asterisk approximate the type of *P. arida* var. *pentaschista.* Plants approximating vars. *arida* and *cerralbensis* are not distinguished here, except for types. MÉXICO: Baja California,—Mcpo. Ensenada, San Francisquito Bay, *Johnston 3544,* 18 May 1921 (GH, K, NY, UC, US); 39mi from Pozo Aleman, *Wiggins 7805,* 28 Feb 1935 (US); Baja California Sur,—Mcpo. Comondú, Comondú, *Bryant s.n.,* no date (US); Magdalena Bay, *Lung s.n.,* no date (UC); Guadalupe Point, Concepcion Bay, *Johnston 4158,* 17 Jun 1921 (GH, US); Las Cuevitas, below Comondu, *Gentry 4453,* 12 Apr 1939 (K, UC, US); S. side of Arroyo San Gregorio, 22.4 km NW of Purisima, *Carter et al. 2483,* 5 Jan 1948 (K, UC, US); 8 mi S. of Río de la Purisima, *Wiggins 15218,* 27 Oct 1959 (GH, UC); *29 mi N. of Villa Constitucion (El Crucero), *Thomas 8405,* 28 Oct 1959 (US); 0.5 mi W. of Rancho Viejo on road to San Javier, *Wiggins & Ernst 558,* 17 Dec 1959 (UC); Vic. of Loreto, *Carter 5885,* 6 Dec 1974 (BM, UC); Vic. of Loreto, *Fuerte 185,* 31 Jan 1984 (UC);—Mcpo. La Paz, *San Jose del Cabo, *Grabendorfer s.n.,* Mar-May (UC); *San Jose del Cabo, *Brandegee 228,* 3 Sep 1890 (UC); *San Jose del Cabo, *Anthony 333,* Mar–Jun 1897 (GH, US [holotype var. *pentaschista*]); La Paz, *Rose 1318,* 14 Jun 1897 (GH, US); La Paz, *Brandegee s.n.,* 17 Oct 1899 (NY); From San Pedro to La Paz, *Nelson & Goldman 7480,* 1 Feb 1906 (US); *San Jose del Cabo, *Rose 16464,* 26 Mar 1911 (US); La Paz, *Johnston 3069,* 12 Apr 1921 (GH, K, US); *Ceralbo Island,

Ruffo's Ranch, *Johnston 4043,* 7 Jun 1921 (GH, *K, NY, UC, US [holotype var. *cerralbensis*]); *La Paz to Ventana, *Collins et al. 92,* 31 Mar 1931 (US); 5.8 mi from La Paz on road to El Coyote, *Porter 125,* 30 Dec 1958 (ARIZ, GH, UC); 15 mi SE of La Paz, *Wiggins 15619,* 25 Nov 1959 (K); 15 mi SE of La Paz, *Wiggins 15662,* 28 Nov 1959 (ARIZ); 22 mi SE of La Paz on road to Las Planes, *Wiggins et al. 458,* 10 Dec 1959 (UC); Arroyo Aguaje, Cerralvo Island, *Moran 9484,* 15 Apr 1962 (US); Sierra de la Giganta, 3.5 km NE of San Jose de Agua Verde, *Carter 4857,* 24 Oct 1964 (GH, UC); Sierra de la Giganta, arroyo at NW base of Cerro Mechudo, *Moran 18980,* 4 Nov 1971 (UC); *12.5 km S. of Todos Santos along Hwy., *Atwood et al. 18979,* 30 Dec 1993 (NY);—Mcpo. Mulegé, Tortuga Island, *Johnston 3598,* 11 May 1921 (GH, US); 3 mi W. of Santa Rosalia, *Wiggins 7948,* 8 Mar 1935 (US); 5 mi N. of Santa Rosalia, *Gentry 3681,* 15 Apr 1938 (ARIZ, GH, UC); 15 mi. N. of San Ignacio, *Hammerly 99,* 29 Sep 1941 (US); 8 mi S. of Santa Rosalia, *Wiggins 11398,* 8 Nov 1946 (GH, UC, US); Isla Tortuga, *Hastings 71-98,* 21 Mar 1971 (ARIZ); 8 mi SE of San Ignacio, *Spjut & Marin 6046,* 26 Mar 1980 (US); Isla Tortuga, *Tenorio 11881,* 15 Aug 1986 (ARIZ); Sonora,— Mcpo. Caborca, E. side of Sierra del Viejo, below Puerto Blanco, *Felger & Gentry 7915,* 20 May 1963 (ARIZ);—Mcpo. Guaymas, Guaymas, *Palmer s.n.,* 1887 (BM); Guaymas, *Palmer 91,* 1887 (GH, NY, US); Guaymas, *Rose 1206,* 5–11 Jun 1897 (GH, NY, US [holotype]); vic. of Guaymas, Las Ranchas, *Rose et al. 15041,* 23 Apr 1910 (US); San Pedro Bay, *Johnston 4298,* 7 Jul 1921 (GH, US); 10 mi N. of Guaymas, *Shreve 7307,* 1 Apr 1935 (NY); Hillside near Miramar, N. of Guaymas, *Waterfall 12839,* 18 Aug 1956 (US); near Guaymas, *Hastings & Turner 64-19,* 26 Apr 1964 (ARIZ); Centinela, vic. of Guaymas, *Felger et al. 10034,* 3 May 1964 (ARIZ); Guaymas, W. of town, *Ripley 14283,* 23 Feb 1966 (NY); 3 mi S. of Bahía Bachocibampo, Guaymas, *Cummins s.n.,* 5 Dec 1971 (ARIZ); San Carlos Bay, W. of Guaymas, *Sanders et al. 2495,* 2 Apr 1982 (UC); Guaymas, *Starr & Starr 193,* 7 Nov 1982 (ARIZ); Canyon Nacapules, *Felger & Reichenbacher 85-1217,* 10 Oct 1985 (ARIZ); Palo Parado, Río Yaqui, 7.3 km SW of Potam, *Felger et al. 85-1408,* 19 Nov 1985 (ARIZ); Playa Miramar, NW part of Guaymas, *Felger & Burquez 92-1015,* 10 Dec 1992 (ARIZ); Cañon las Barajitas, Sierra el Aguaje, 18 km NW of San Carlos, *Felger & Wilson 95-127,* 16 Feb 1995 (ARIZ); —Mcpo. Hermosillo, Hermosillo, *Maltby 206,* 10 Jun 1897 (NMC, US); San Esteban Island, *Johnston 4402,* 19 Apr 1921 (US); San Esteban Island, *Johnston 3200,* 20 Apr 1921 (GH, US); San Esteban, *Felger 7039,* 5 Apr 1963 (ARIZ); N. side of Isla San Esteban, *Felger & Cooper 15448,* 21–22 Dec 1966 (ARIZ); 2.7 mi SE of Punta Chueca, *Van Devender & Kearns s.n.,* 16 Feb 1977 (ARIZ); Arroyo Limantur, Isla San Esteban, *Wilkinson 159,* 13 Oct 1977 (ARIZ); San Esteban Island, *Moran 28172,* 20 Mar 1980 (DES); 2 mi NW of Kino Bay, *Van Devender 90-523,* 12 Sep 1990 (ARIZ); Arroyo Limantur, Isla San Esteban, *Van Devender 92-480,* 29 Apr 1992 (ARIZ); Cerro la Cantera, Rancho la Poza, 20 km S. of Hermosillo, *Van Devender & Penalba 95–538,* 29 May 1995 (ARIZ);—Mcpo. Huatabampo, *Loma de Moroncarit, 2 km S. of Etchoropo, *Jenkins et al. 88-98,* 11 Oct 1988 (ARIZ); *7.5 km S. of Huatabampo (Calle Juarez), *Sanders et al. 9254,* 4 Sep 1989 (ARIZ);—Mcpo. Navojoa, *Arroyo Masiaca, ca. 0.5 km N. of Teachive de Masiaca, *Van Devender et al. 93-950,* 21 Sep 1993 (ARIZ);—Mcpo. Pitiquito, Punto Cirio, 6 mi S. of Puerto Libertad, *Turner & Lowe 60-1,* 3280, 15 Apr 1960 (ARIZ); 3.5 mi NE of Desemboque, *Felger et al. 17416,* 23 Feb 1968 (ARIZ); 0.4 mi E of Punta Cirio, Sierra Bacha, S. of Puerto Libertad, *Van Devender 92-464,* 19 Apr 1992 (ARIZ);— Mcpo. Trincheras, Cerro los Trincheras, S. of Trincheras, *Gillespie & Martin s.n.,* 9 Nov 1985 (ARIZ);—Undetermined localities in Sonora, Verrugo Pass, *MacDougal & Shreve 1,* 14 Nov 1923 (US); NW Sonora, *Pringle 52,* 18 Aug 1884 (GH); Undetermined localities in Mexico, *Brandegee s.n.,* no date (UC); Baja California, *Diguet s.n.,* no date (US); USA: Arizona,—Pima Co., *Gates Pass, *Spellenberg & Zucker 12959,* 17 Aug 1999 (NMC); *Arizona-Sonora Desert Museum, *Emmett s.n.,* Aug 2000 (BH); *Gates Pass, *Jenkins s.n.,* 19 Oct 2000 (BH); *Gates Pass, *Goldman 2092,* 30 Aug 2001 (BH); *Naturalized in the yard of Katherine Waser, in Tucson, *Goldman 2303,* 25 Oct 2002 (BH); CULTIVATED MATERIAL: *Seedlings, cultivated at the University of Rochester, Rochester, NY, from seed from Reddington Pass, between the Santa Catalina and Rincon Mts., near Tucson, AZ, *Goldman 1541,* 28 Aug 2000 (BH); *Cultivated at the teaching greenhouse at the University of Connecticut, Storrs, seed originally obtained in 1999 by John Maugeri from the Passiflora Society International, *Goldman 1754,* Apr 2001 (BH); *Cultivated at Cornell University, from seed from Reddington Pass, between the Santa Catalina and Rincon Mts., near Tucson, AZ, *Goldman 1712,* 1 Apr 2001 (BH); *as in *D.G. 1712, Goldman 1709,* 20 Apr 2001 (BH); *Cultivated at Cornell University, from seed obtained by the staff of the Desert Botanical Garden on 12 Oct 1987 from the E. slope of Las Guijas Mts., *Goldman 1747,* 4 May 2001 (BH); *Cultivated at Cornell University, from seed from the grounds at the Sonora Desert Museum, Tucson, *Goldman 1748,* 5 May 2001 (BH); *Cultivated at the University of Rochester, from seed from Tohono Chul Park, their source being the Coyote Mts. near Mendoza Canyon., *Goldman 1749,* 10 May 2001 (BH); *Cultivated at Cornell University, Ithaca, NY, but originally from seed collected in Nov 2000 from a plant invading a greenhouse at the Desert Botanical Garden, Phoenix; *Goldman 1756;* 8

Jun 2001 (BH); *as in *D.G. 1749, Goldman 1792*; 4 Aug 2001 (BH).

Passiflora arizonica

MÉXICO: Sonora,—Mcpo. Alamos, Los Promontorios, *Russell & Souviron 10,* 10 Aug 1930 (US); Congrejos, near Alamos, *Walker 70038,* 26 Aug 1970 (K); 0.6 mi S. of Alamos, *Fish 106,* 12 Sep 1973 (UC); E. side of Alamos, *Martin & McWhorter s.n.,* 5 Aug 1990 (ARIZ); S. of Alamos, *Yetman et al. s.n.,* 5–8 Nov 1992 (ARIZ); Sierra de Alamos, *Steinmann & Meyer 970,* 1 Sep 1996 (ARIZ, NY),—Mcpo. Altar, Sierra del Pozo Verde, *Schott s.n.,* 18 Jul 1855 (NY),—Mcpo. Bacadéhuachi, El Coyote, *Felger 3627,* 23 Jul 1960 (ARIZ),—Mcpo. Cucurpe, 8.7 mi ENE of Cucurpe, *Toolin & Van Devender s.n.,* 3 Oct 1979 (ARIZ),—Mcpo. Guaymas, S. of Guaymas, *Waterfall 12855,* 19 Aug 1956 (GH, US); S. of Guaymas, *Bates & Vivaldi 3338,* 23 Oct 1973 (BH, K, NY, US); Hwy 15, 8.8 mi N. of turnoff to Bahía San Carlos, *Felger & Reichenbacher 85-1592,* 12 Oct 1985 (ARIZ); 2.3 km by road SE of Rancho El Tigre, *Felger & Straub 85-1458,* 21 Nov 1985 (ARIZ); vic. 28°07′N, 111°03′W, *Felger et al. 85-1535,* 30 Dec 1985 (ARIZ),—Mcpo. Hermosillo, 10 mi S. of Hermosillo, *Gentry 4553,* 6 Sep 1939 (ARIZ); 8 mi W. of Hermosillo, *Wiggins & Rollins 94,* 17 Aug 1941 (ARIZ, GH, NY, UC, US); Sierra Libre, 7.4 mi S. of La Pintada, *Van Devender s.n.,* 9 Feb 1978 (ARIZ); 43 mi N. of Guaymas, 1.3 mi NE of hwy. 15, *Maskarinec & Hodgson 3007,* 28 May 1984 (DES),—Mcpo. Huatabampo, Los Cerritos, ca. 40 mi S. of Navajoa, *Gentry 14389,* 1–3 Oct 1954 (ARIZ, US); 40 mi S. of Navajoa, *Solbrig & Ornduff 4403,* 7 Aug 1957 (NY),—Mcpo. Imuris, 11 mi E. of Imuris, *Hill 73H59,* 23 Aug 1973 (NY),—Mcpo. Ures, 10 mi. NE of Ures, *Shreve 6714,* 20 Sep 1934 (ARIZ); 9.5 mi NE of Ures, *Wiggins 7347,* 20 Sep 1934 (US),—Mcpo. Villa Hidalgo, Canyon del Agua Amarga, *White 3607,* 30–31 Aug 1940 (ARIZ, GH); USA: Arizona,—Pima Co., Fresnal Canyon, Baboquivari Mts., *Harrison 4774,* 26 Sep 1927 (US [holotype]); Fresnal Canyon, Baboquivari Mts., *Gilman 78,* 2 Sep 1931 (GH, NY); Baboquivari Mts., between Fresnal Canyon and Toro Canyon, *Gilman B78,* 14 Sep 1931 (US); Baboquivari Mts., *Peebles 8806,* 2 Aug 1932 (ARIZ, BM, GH, US); Fresnal, *Harrison & Hope 9048,* 11 Sep 1932 (ARIZ); Baboquivari Mts., above Forest Cabins, *Goodding s.n.,* 7 Oct 1936 (US); Fresnal Canyon, Baboquivari Mts., *Darrow 82,* 2 Aug 1937 (K, US); Coyote Mts., *Hester s.n.,* 30 Sep 1937 (ARIZ); Baboquivari Canyon, *Kearny & Peebles 14972,* 1 Sep 1940 (ARIZ); Mt. Baboquivari, *Gould et al. 2704,* 7 Oct 1944 (ARIZ); Rocky slope along trail to top of Baboquivari Mtn., *Gould & Haskell 3241,* 31 Aug 1945 (ARIZ, NY, UC, US); Las Guijas Mts., T21S, R10E, Sec. 5, *Engard & Haughey 1064,* 19 Aug 1977 (DES); 1 mi N. of

Arivaca, grasslands, 4000 ft, *Couch & Mittleman s.n.,* 22 Aug 1978 (DES, NY); Desert Botanical Garden, *Gass s.n.,* 15 Aug 1979 (DES); Thomas Canyon, Baboquivari Mts., *Toolin & Yatskievych 457,* 15 Sep 1979 (ARIZ); Baboquivari Canyon, Baboquivari Mts., *Toolin & Reichenbacher 1410,* 16 Jun 1981 (ARIZ); Las Guijas Mts., T21S, R10E, Sec. 17, *Mittleman 307,* 1 Sep 1982 (ARIZ, DES); Baboquivari Mts., Virtud Tank area, *Mittleman 565,* 23 Sep 1982 (ARIZ, DES); Baboquivari Mts., within ¾ mi. of Thomas Canyon, *Quirk & Hodgson 4005,* 12 Sep 1985 (DES); Tohono O'odoham Reservation, Baboquivari Mts., Baboquivari Canyon, *Hodgson et al. 5079,* 15 Jul 1988 (DES); Buenos Aires NWR, ca. 5.3 mi SE of Refuge Headquarters along road to Yellowjacket Dam, *McLaughlin 4830,* 30 Jul 1988 (ARIZ); Above Mesquite Root Dam, S. side of Las Guijas Mts., *McLaughlin 4863,* 6 Aug 1988 (ARIZ); Pozo Verde Mts., NW ¼ Sect. 7, T22S, R8E, elev. 3900 ft, *McLaughlin 5385,* 25 Sep 1988 (ARIZ); Las Guijas Mts., *McLaughlin 6036,* 24 Aug 1990 (ARIZ); Baboquivari Mts., Brown Canyon, *Fishbein & Quinn 2891,* 26 Oct 1996 (ARIZ); SW of the Yellow Jacket Dam, Buenos Aires National Wildlife Refuge, *Goldman 2120,* 1 Sep 2001 (ARIZ, BH, GH, MEXU, MO); —Santa Cruz Co., California Gulch, just below cemetery, *Kaiser & Bache-Wiig 1283,* 2 Jun 1979 (ARIZ); E. side of Holder Canyon, 0.6 mi NNW of Bartlett Mtn., *Van Devender & Toolin s.n.,* 29 Oct 1981 (ARIZ); E. side of Old Glory Canyon and Warsaw Canyon, Coronado National Forest, *Goldman 2109,* 31 Aug 2001 (ARIZ, BH, GH, MEXU, MO); CULTIVATED MATERIAL: Seedlings, cultivated at Cornell University, from seed from Coronado National Forest [=*Goldman 2109*], *Goldman 2306,* 1 Jun 2002 (BH, GH, MO); Seedlings, cultivated at Cornell University, from seed from Buenos Aires National Wildlife Refuge (=*Goldman 2120*), *Goldman 2307,* 1 Jun 2002 (ARIZ, BH, DES, GH, MEXU, MO, NY, US); Cultivated at Cornell University, started from seed from Coronado National Forest (=*Goldman 2109*), *Goldman 2304,* 6 Aug 2002 (BH, GH); Cultivated at Cornell University, started from seed from Buenos Aires National Wildlife Refuge (=*Goldman 2120*), *Goldman 2305,* 6 Aug 2002 (BH, GH, MO).

Passiflora chrysophylla

ARGENTINA: Formosa, Las Lomitas, *Parodi 8400,* 24 Jan 1928 (GH); Beruejo, *Pierotti 40XX,* 30 Sep 1945 (K); BOLIVIA: Andres Ibanez,—Mcpo. Santa Cruz, 6 km NW of Terevinto, *Nee & Coimbra 36995,* 30 Nov 1988 (NY); PARAGUAY: Asuncion, Asuncion, *Morong 223,* 21 Dec 1888 (NY); Asuncion, *Gibert 1031,* Jan 1877 (K; holotype *P. chrysophylla* var. *sericea* Chodat); Caaguazu, cerca y al N de Yhú, *Casas & Molero 6375,* 21 Feb 1982 (NY); Central, Villa Elisa, *Pedersen 3123,* 22 Jan 1955 (K); Nemby, *Vavrek & Vavrek*

467, 25 Nov 1981 (NY); Concepcion, Prope Concepcion, *Hassler 7418,* 1901/1902 (BM); In regione cursus superioris fluminis Apa, *Hassler 7804,* 1901/1902 (BM); Prope Concepcion, *Hassler 7547,* Sep 1902 (BM, K, NY); isotypes of *P. chrysophylla* var. *concepcionis* Chodat. & Hassl.); between Río Apa and Río Aquidaban, *Fiebrig 4825, 5286,* 1908/1909 (BM, K, GH); Parque Nacional San Luis de la Sierra, Arroyo Tagatiya-Guazu, *Zardini & Ramirez 41390,* 14 Oct 1994 (NY); Cordillera, Tobati, Ybytu Silla mesa, *Zardini & Velazquez 26203,* 8 Feb 1991 (NY); San Pedro, Alto Paraguay, Primavera, *Woolston 480,* 15 Mar 1955 (K, NY); Alto Paraguay, Primavera, *Woolston 1210,* 20 Sep 1960 (K, NY);—Undetermined localities in Paraguay, in regione cursus superioris fluminis Y-acá, *Hassler 6878,* 1900 (BM); western bank of Río Paraguay, *Hassler 2360,* Oct 1903 (BM, GH, K, NY); About 23S, 59W, *Carter s.n.,* 1927 (BM).

Passiflora foetida var. *acapulcensis*

MÉXICO: Guerrero,—Mcpo. Acapulco, Acapulco, *Palmer 306,* Oct 1894 to Mar1895 (NY, UC, US); Acapulco, *McDaniels 132, 162, 164,* 21 Aug 1935 (BH); Puebla,—Mcpo. Acatlan, 11 km SE de Acatlan de Osorio, *Sousa 8207,* 18 Oct 1977 (NY).

Passiflora foetida var. *ciliata*

MÉXICO: Campeche,—Mcpo. Palizada, 27.8 mi E. of La Veleta, *Lloyd & Mueller 3690,* 17 Jun 1965 (UC); Yucatan,—Mcpo. Progreso, Progreso, *Gaumer 23355,* Apr 1916 (GH).

Passiflora foetida var. *foetida*

MÉXICO: San Luis Potosi,—Mcpo. Tamazunchale, Tamazunchale, *Kenoyer s.n.,* 1 Sep 1938 (ARIZ). UNDETERMINED LOCALITY: *no collector s.n.,* no date (LINN [holotype]). According to Killip (1938), the typical variety of *P. foetida* is not supposed to be in Central America, but the above Mexican specimen roughly fits the morphological description.

Passiflora foetida var. *gossypiifolia*

Passiflora foetida var. *longipedunculata* Killip is here included in var. *gossypiifolia* (e.g., *Johnston 3660* and *Bartlett 10987*). ARGENTINA: Cordoba, *Kuntze s.n.,* Jul 1891 (NY); Salta,—Mcpo. Gral Guemes, Unchime, *Meyer 22579,* 18 Mar 1965 (NY);—Mcpo. Rivadavia, J. Solá (Morillo), *Maranta & Arenas 166,* 21 Jan 1983 (NY); Tucuman,—Mcpo. Burrayaco, El Cajon, *Venturi 10338,* 16 Mar 1930 (GH);—Undetermined localities in Tucuman, Pasando El Arsenal, *Meyer 22326,* 8 Jan 1965 (NY); BOLIVIA: Caballero,—Mcpo. Santa Cruz, 9 km SE of Comarapa, *Nee 46547,* 28 Dec 1995 (NY);—Undetermined locality in Caballero. Saipina, Cerro Buena Vista y Monte Grande, *Vargas et al. 2417,* 11 May 1993 (NY); GUATEMA-

LA: Izabal, Quirigua, *Standley 23968,* 15–31 May 1922 (GH); Zacapa, 20 km al E de Zacapa, *Garcia et al. 1368,* 4 Nov 1989 (BM); MÉXICO: Baja California,—Mcpo. Ensenada, Arroyo San Pablo, Santa Gertrudis, *Purpus 122,* Jan to Mar 1898 (UC); Baja California Sur,—Mcpo. Comondú, Comondú, *Brandegee s.n.,* 1 Mar 1889 (UC); Comondú, *Brandegee s.n.,* 11 Mar 1889 (UC);—Mcpo. La Paz, near San Jose del Cabo, *Bailey 225,* 2 Apr 1936 (BH, US);—Mcpo. Mulegé, Mulegé, *Johnston 3660,* 14 May 1921 (US); 35 mi N. of San Ignacio, *Nelson & Goldman 7194,* 4 Oct 1904 (US); 5 mi W. of Santa Rosalia, *Shreve 7059,* 8 Mar 1935 (ARIZ); 3 mi W. of Santa Rosalia, *Wiggins 7948A,* 8 Mar 1935 (NY); 25 km WNW of Ej. Alfredo Bonfil, *Reina et al. 2002-150,* 10 Mar 2002 (BH); 25 km WNW of Ej. Alfredo Bonfil, *Reina et al. 2002-156,* 10 Mar 2002 (BH); 3.5 km E. of San Ignacio, *Reina et al. 2002-168,* 11 Mar 2002 (BH); 5 km E. of San Ignacio, *Reina et al. 2002-171,* 11 Mar 2002 (BH); 5 km E. of San Ignacio, *Reina et al. 2002-174,* 11 Mar 2002 (BH);—Undetermined localities in Baja California Sur, 10 mi S. of Mision Dolores, *Wiggins et al. 314,* 5 Dec 1959 (GH); Mesa de San Geronimo, *Carter 5011,* 23 Sep 1965 (UC); Arroyo de la Higuera, NE base of Cerro Giganta, *Carter & Sousa 5217,* 19 Oct 1966 (UC); Chiapas,—Mcpo. Motozintla, between Mazapa and Motozintla, *Matuda 4811,* 19 Jul 1941 (NY);—Undetermined locality in Chiapas, Jalisco, *Purpus 9258,* Aug 1923 (GH); Chihuahua,—Mcpo. Batopilas, Hacienda San Miguel, near Batopilas, *Palmer 199,* Sep 1885 (GH, K, US); Tres Hermanos, SE of Batopilas, *Hewitt 33,* 5 Mar 1945 (GH); N side of Barranca de Batopilas, *Bye 3202,* 23 Jan 1973 (GH); N side of Barranca de Batopilas, *Bye 3621,* 24 Apr 1973 (GH); NE of Batopilas, *Tenorio & Torres 4436,* 16 Sep 1983 (ARIZ); La Bufa, *Tenorio & Romero 6607,* 18 Jul 1984 (ARIZ); Coahuila, Muzquiz, *Marsh 479,* 11 Jul 1936 (GH); Colima,—Mcpo. Colima, Colima, *Palmer 281,* Jul 1897 (US); Guerrero,—Mcpo. Acapulco, Acapulco and vicinity, *Palmer 306,* Oct 1894 to Mar 1895 (GH);—Mcpo. Adama, Temisco, *Mexia 8747,* 5 Nov 1937 (BH, GH, K, UC);—Mcpo. Coyuca, Cutzamala-Rancho, *Hinton 8045,* 12 Jul 1935 (GH, K); Jalisco,—Mcpo. Bolaños, Bolaños, *Rose 2894,* 10–19 Sep 1897 (US);—Mcpo. Guadalajara, Guadalajara, *Oliver et al. 664,* 13 Jul 1971 (BH);—Mcpo. Sayula, Sayula, *Jones 354,* 26 May 1892 (US);—Undetermined locality in Jalisco, Orendalin, *Jones 27462,* 27 Nov 1930 (BM, NY, US); Mexico,—Mcpo. Temascaltepec, Tejupilco, *Hinton 3659,* 27 Mar 1932 (DES); Volcan, *Hinton 992,* 8 Jul 1932 (BM, DES, K, NY); Ipericones, *Hinton 8076,* 20 Jul 1935 (ARIZ, GH, K); Michoacan,—Mcpo. Apatzingen, Tepalcatepec, *Hinton 12107,* 26 Aug 1938 (GH, K);—Mcpo. Hutamo, Tacupa, *Hinton 5514,* 20 Jan 1934 (GH, K);—Mcpo. Zitacuaro, Zitacuaro, San Jose Purua, *Hinton 13049,* 22 Jul 1938 (GH, K); Morelos,—Mcpo. Cuernavaca, Cuerna-

vaca, *Bilimek 752,* 20 Mar 1866 (BM, K, NY); Nayarit,—Mcpo. Acaponeta, Acaponeta, Tepic, *Lamb 529,* Feb 1895 (GH, NY); Acaponeta, Tepic, *Rose 1466,* 25 Jun 1897 (GH); Acaponeta, Tepic, *Rose et al. 14276,* Apr 1910 (GH); Nuevo Leon,—Mcpo. Cienega de Flores, along Mex. hwy 85 at bridge crossing of Río Salinas at Cienega de Flores, *Andres & Wyland 3,* 8 Nov 1985 (BH);—Mcpo. Sabinas Hidalgo, Ojo de Agua, *Chase 7055,* 18 Jun 1939 (GH);—Mcpo. Villa Santiago, Las Ajuntas, *Mueller 2994,* 24 Aug 1939 (GH);—Undetermined localities in Nuevo Leon, Hills near Monterrey, *Pringle 2238,* 7 Jun 1888 (GH); 30 mi S of Monterrey, *Mueller & Mueller 1310,* Aug 1934 (GH); Cerro de la Silla, Monterrey, *White & Chatters 172,* 4 Sep 1937 (GH); Oaxaca, near Oaxaca, *Conzatti 152,* 17 May 1896 (GH); Valley of Oaxaca, *Pringle 13763,* 16 May 1906 (GH); Picacho-San Geronimo, *Purpus 1903,* Oct 1913 (BM, GH); above San Flipe, near Oaxaca, *Sharp 45911,* 6 Sep 1945 (GH); 65 mi S of Oaxaca on road to Tehuantepec, *Morley 678,* 15 Jul 1946 (GH);—No locality in Oaxaca, *Smith 465,* 28 Jun 1895 (GH); Puebla,—Mcpo. Zinactapec, 14 km E. of San Sebastian Zinactapec, *Tenorio et al. 17174,* 23 Sep 1990 (NY); Quintana Roo,—Mcpo. José María Morelos, Lake Chichankanab, *Gaumer 23639,* Apr 1917 (GH); Sinaloa,—Mcpo. Culiacan, Culiacan, *Brandegee 9532,* 12 Sep 1904 (GH, US); Imala, *Gentry 4985,* 19 Nov 1939 (ARIZ);—Mcpo. Elota, El Norote, *Ortega 5909,* 1925 (US);—Mcpo. Mazatlan, vicinity of Mazatlan, *Rose et al. 13688,* 30 Mar 1910 (NY, US); Mazatlan, Signal Hill, *Mexia 49.5,* 16 Sep 1925 (UC); Mazatlan, *Ortega 7230,* Jul 1934 (K, US);—Undetermined locality in Sinaloa, Rancho La Tasajera, *Narvaes & Salazar 878,* 25 Sep 1919 (US); Sonora,—Mcpo. Alamos, vicinity of Alamos, *Rose et al. 12931,* 16 Mar 1910 (US); San Bernardo, *Gentry 1679,* 7 Sep 1935 (GH, K); Alamos, Río Fuerte, *Gentry 2257,* 22 Jun 1936 (K, US); 25 km W. of Alamos, *Meyer s.n.,* 7 Aug 1992 (ARIZ); Below the village of Guajaray, *Van Devender et al. 93-469,* 19 Mar 1993 (ARIZ);—Mcpo. Etchojoa, 15 km E. of Navajoa, *Sanders et al. 9263,* 5 Sep 1989 (ARIZ);—Mcpo. Navojoa, 6.5 km WNW of San Jose de Masiaca, *Van Devender et al. 92-1110,* 8 Oct 1992 (ARIZ); 6.5 km WNW of San Jose de Masiaca, *Steinmann et al. 93-359,* 22 Nov 1993 (ARIZ);—Mcpo. Yecora, 9.3 km E. of Tepoca, *Van Devender et al. 2000-516,* 30 Aug 2000 (ARIZ);—Undetermined localities in Sonora, Cerro Prieto, *Tenorio & Torres 4627,* 1 Oct 1983 (ARIZ); between Navajoa and Alamos, *Martin s.n.,* 18 Dec 1989 (ARIZ); Tamaulipas,—Mcpo. Tampico, vicinity of Tampico, *Palmer 193,* 10 Mar to 19 Apr 1910 (BM, GH, K); vicinity of Tampico, *Palmer 487a,* 1–22 May 1910 (GH, K);—Mcpo. Victoria, 14 mi SW of Ciudad Victoria, *Webster et al. 11250,* 9 Jun 1962 (GH);—Undetermined localities in Tamaulipas, vic. Of El Mulato, *Bartlett 10987,* 16 Aug 1930 (NY, US [holotype of *P. foetida* L. var. *lon-*

gipedunculata Killip]); near Villa Juarez, *Perkins & Hall 3174,* 31 Mar 1939 (BH); Veracruz, Orizaba, *Botteri 996,* no date (GH); Zacatecas, near San Juan Capistrano, *Rose 2443,* 20 Aug 1897 (GH); NICARAGUA: Depto. Rivas, Island Ometepe, Lake Nicaragua, *Smith s.n.,* Jan 1893 (UC); USA: Texas—Calhoun Co., Green Lake, *Tharp s.n.,* 2 Jul 1938 (GH, NY); Port Lavaca, *Fisher s.n.,* 13 Aug 1939 (BRIT);—Cameron Co., Río Hondo, *Chandler 7000,* Jun 1913 (GH, NY, UC, US); Olmito, *Rose & Russell 24170,* 23 Oct 1927 (US); E. of Los Indios, *Correll & Wasshausen 27679,* Jun 1963 (GH);—Frio Co., Moore, *Parks 17480,* Dec 1935 (GH);—Hidalgo Co., Elcouch, *Blakeney s.n.,* 11 Oct 1942 (GH); near La Joya, *Walker 94,* 5 Jun 1944 (BRIT, GH); 1 ½ mi E. of La Joya P.O., *Cory 51340,* 29 Nov 1945 (GH, NY); near Puerto Rico, *Tharp et al. 51-1648,* 26 Jul 1951 (BRIT); 0.2 mi W. of Puerto Rico, *Tharp & Johnston 541869,* 9 Oct 1954 (BRIT); Delta Lake, *Wimberly 21,* 27 Oct 1979 (BRIT); just S. of Mission, *Churchill 90-750,* 20 Sep 1990 (BRIT);—Jim Wells Co., 6 mi W. of Alice, *Gould & Kapadia 8853,* 15 Sep 1959 (BRIT);—Kenedy Co., Yturria, *Lundell & Lundell 8739,* 6 May 1940 (US);—Maverick Co., Eagle Pass, *Havard s.n.,* 1882 (GH, PH);—Nueces Co., vic. Of Corpus Christi, *Rose 18084,* Oct 1913 (US); —San Patricio Co., 7 ½ mi S. of Taft, *Jones 643,* 5 Oct 1951 (BRIT);—Starr Co., near Río Grande City, *Mcalley 203,* 1889 (PH);—Webb Co., Laredo, *Nickles s.n.,* 1879 (PH); Laredo, *Palmer 2110,* Aug 1879 (GH, K); near Laredo, *MacKenzie 12,* Aug 1899 (BRIT, NY, US); 14 mi E. of Laredo, *Ramirez et al. 8688,* 11 Nov 1962 (BRIT); 12.5 mi S. of Laredo, *Trevino et al. 8765,* 21 Nov 1962 (BRIT); —Willacy Co., El Jardin, *Runyon 445,* 10 Jul 1923 (US); no locality, *Tharp s.n.,* 26 Jun 1941 (GH);—Zapata Co., 2.6 mi W. of Zapata, *Villarreal 26,* 5 Aug 1963 (BRIT);—Undetermined locality in Texas, below Doñana, *Parry et al. 392,* no date (GH, NY, US); CULTIVATED MATERIAL: Cultivated at the University of Rochester, Rochester, NY, from seed obtained in the yard of Alfred Richardson in Brownsville, TX, *Goldman 1609,* 1 Dec 2000 (BH); Cultivated at Cornell University, Ithaca, NY, from seed obtained in the yard of Alfred Richardson in Brownsville, Texas, *Goldman 1713,* 1 Apr 2001 (BH); as in *Goldman 1713, Goldman 1710,* 20 Apr 2001 (BH); as in *Goldman 1713, Goldman 2225,* 28 Dec 2001 (BH); Cultivated at Cornell University, originally from 3 mi SW of Mathis, San Patricio Co., Texas, *Goldman 2308,* 22 Jun 2002 (BH).

Passiflora foetida var. *hastata*

GUATEMALA: swamp at Morales, *Deam 6028,* 29 May 1909 (GH); MÉXICO: Chiapas—Mcpo. Escuintla, Esperanza, Esquintla, *Matuda s.n.,* 14 Jul 1947 (GH);—Mcpo. Tapachula, Canton Gradalupe, *Ventura & Lopez 1996,* 25 Jun 1985 (NY); Hidal-

go—Mcpo. Huazalingo, between Huazalingo and Tehuetlan on road to Huejutla, *Moore 3042,* 30 May 1947 (BH); Oaxaca—Distr. Comaltepec, Vista Hermosa, *Martinez 847,* 27 May 1966 (NY);—Distr. Juchitan, Juchitlan, *MacDougall H314,* 3 Mar 1972 (NY); Palomares, Juchitlan, *MacDougall s.n.,* 1 Apr 1973 (NY);—Distr. Tuxtepec, Ciltepec and vic., *Martinez 3,* Jul 1940 to Feb 1941 (GH); Puebla—Mcpo. Huaytamalco, San Jose Acateno, *Marquez 612,* 22 Mar 1976 (NY); Tabasco,—Mcpo. Centro, 14 mi SE of Villahermosa, *Fryxell 736,* 8 Sep 1968 (NY);—Mcpo. Huimanguillo, km 10.4 de la desvacion de Huimanguillo, *Cowan 3325,* 27 Jun 1981 (NY); Veracruz,—Mcpo. Atzalan, Novaro, *Ventura 19732,* 9 Sep 1982 (BH);—Mcpo. Chalcaltianguis, 12 km SW of Cosamalopan, *Nee & Taylor 29279,* 2 Feb 1984 (NY);—Mcpo. Coatzacoalcos, Fortuño, Coatzacoaltos River, *Williams 8330,* Mar 1937 (US);—Mcpo. Hueyapan de Ocampo, Zacuapan, *Purpus s.n.,* no date (BM, GH, K, NY); Zacuapan (cultivated in Washington, DC.), *Purpus s.n.,* no date (GH); Zacuapan, *Purpus s.n.,* Jun 1921 (US);—Mcpo. Martinez de la Torre, 10 km W of San Rafael, *Barrie & Luckow 1461,* 9 Oct 1986 (NY);—Mcpo. Mecayapan, 7 km S. of Tatahuicapan, *Nee et al. 25127,* 16 Jul 1982 (NY);—Mcpo. Misantla, Independencia, *Ventura 985,* 27 Apr 1970 (NY);—Mcpo. Papantla, Tajin, *Kelly 51,* 1947 (BH); Tajin, *I. Kelly 116,* 1947 (BH);—Mcpo. Vega de Alatorre, 6 km NW of emilio Carranza, *Nee & Taylor 26987,* 29 Apr 1983 (NY);—Undetermined locality in Veracruz, *Linden 750,* 1838 (K).

Passiflora foetida var. *hibiscifolia*

MÉXICO: Chiapas,—Mcpo. Tonala, Paderon, Tonala, *Matuda 16318,* 14–20 Jan 1948 (US; Guerrero,—Mcpo. Acapulco, Acapulco and vic., *Palmer 409,* Oct 1894 to Mar 1895 (GH, US); N of Pie de la Cuesta, NW of Acapulco, *Barkley 4171,* 5 Jan 1944 (GH);—Mcpo. Adama, Temisco, *Mexia 8911,* 27 Nov 1937 (GH, K, UC, US); Oaxaca,—Distr. Cuicatlan, Cuicactan, *Smith 189,* 24 Sep 1894 (GH); vic. of Cuicatlan, *Nelson 1632,* 8–24 Oct 1894 (GH, US); Cuicactan, *Conzatti 184,* 23 Jun 1896 (GH); Tomelin Canyon, *Rose & Hough 4676,* 23 Jun 1899 (US); near Tomelin, *Rose et al. 10056,* 4–5 Sep 1905 (US); Cuyamecalco, Cuicactlan, *Aguirre 12,* Dec 1945 (NY);—Distr. Juchitlan, Carretera Juchitlan-Ixtepec, *Kelly 962,* 3 Mar 1957 (UC);—Distr. Mixe, 2 km SE Vista Hermosa, *Torres 108,* 13 Mar 1982 (NY);—Distr. San Mateo del Mar, San Mateo del Mar, *Zizumbo & Colunga 67,* 11 Jan 1978 (UC);—Distr. Tehuantepec, Huilotepec, *Nelson 2589,* 4–11 May 1895 (GH, US); Tehuantepec, *Orcutt 5272,* 2 Jun 1910 (US); 9–10 km E. of La Ventosa, *King 1686,* 16 Jul 1959 (NY, UC, US); Tehuantepec, *MacDougall s.n.,* Dec 1964 (NY); Tehuantepec, *MacDougall 25.S,* 28 Mar 1970 (NY); Tehuantepec, *MacDougall s.n.,* 31 May

1970 (NY); Salina Cruz, La Ventosa, *MacDougal 314,* 27 Jul 1978 (US);—Undetermined localities in Oaxaca, San Antonio Valley, *Smith 245,* 1 Sep 1894 (UC, US); River banks, San Antonio, *Pringle 4847,* 2 Sep 1894 (BM, GH, K, NY, US); Tehuantepec fluises, *Harms 1665,* 10 Jan 1896 (NY); Tehuantepecfluoses, *Seler 1665,* 10 Jan 1896 (GH, K); Santa Catarina, *Rusby 48,* 16 Jul 1910 (NY, US); 24 mi E of Totalapan, *Webster et al. 12996,* 12 Aug 1962 (GH); Puebla,—Mcpo. Coxcatlan, 1 mi N. of Tlapa, *MacDougal 285,* 20 Jul 1978 (US);—Mcpo. San Antonio Nanahuatipan, Cañada Bandera, *Tenorio et al. 8861,* 28 May 1985 (US; Yucatan,—Undetermined locality, Mayan temple ruins, *Degener & Degener 26768,* 29 Sep 1959 (NY); NICARAGUA:—Distr. Grenada, Grenada, *Baker 74,* 11 Feb 1903 (GH).

Passiflora foetida var. *hirsutissima*

GUATEMALA: Alta Verapaz,—Dpto. Sepacuite, *Owen 9,* Oct 1901 (US [holotype]).

Passiflora foetida var. *lanuginosa*

GUATEMALA: Peten, 1 km from Santa Elena, *Lundell 5737,* 12 May 1966 (GH); MÉXICO: Campeche,—Mcpo. Champoton, Tuxpeña, *Lundell 1034,* 10 Dec 1931 (UC, US); Chiapas,—Undetermined locality, La Roblada, *MacDougall H492,* 7 Jun 1972 (NY); Oaxaca,—Distr. Centro, 8.5 mi NE of Valle Nacional, *Thurm et al. 242,* 10 Aug 1979 (NY);—Distr. Tuxtepec, Outskirts of Tuxtepec, *Nelson 373,* 9 Apr 1894 (US);—Undetermined locality in Oaxaca, near Santo Domingo, *Nelson 2703,* 18 Jun 1895 (GH, US); San Luis Potosi,—Mcpo. Ciudad Santos, near Tancanhuitz, *Nelson 4381,* 1 May 1898 (GH, NY);—Mcpo. Ciudad Valles, San Dieguito, *Palmer 124,* 13–16 Jun 1904 (GH, K, NY, US); Valles, *Fisher 3342,* 17 Jul 1933 (GH, US); Paso de Abra, near Ciudad Valles, *LeSueur 310,* Aug 1938 (ARIZ); bank of Río Valles, *Leavenworth 204,* 27 Jun 1940 (ARIZ, GH, NY); S. of Ciudad Valles, *Fryxell 1078,* 18 Jun 1969 (NY); El Banito, 6.5 mi S. of Ciudad Valles, *Thomas et al. 2805,* 27 Jun 1982 (UC);—Mcpo. Tamazunchale, Tamazunchale, *Moore 6,* 22 Sep 1940 (BH, GH); 6 mi N of Tamazunchale, *Kenoyer & Crum 3967,* 4 Sep 1948 (GH);—Mcpo. Xilitla, 3 mi S. of Xilitla, *Ward 7797,* 1 Jun 1971 (NY); just E. of Xilitla, *LeDoux 2499,* 26 May 1979 (NY);—Undetermined localities in San Luis Potosi, Las Palmas, *Rose & Hough 4875,* 14 Jul 1899 (US); Mountain pass between Valles and Guerrero, *Atchison 453,* 30 May 1948 (BH); El Salto Falls, *Shutt & Drawe 51,* 15 Jun 1951 (BRIT); 5 mi W. of El Mecca, *Blume & Burdine 529,* 17 Jun 1951 (BRIT); El Salto Falls, *Daniel & Meschledt 369,* 18 Jun 1951 (BRIT); El Salto, *Kenoyer & Crum 4028,* 2 Sep 1953 (GH); Tamaulipas,—Mcpo. Tampico, vic. Of Tampico, *Palmer 21,* 1–31 Jan, 1910 (BM, GH, K, NY); vic. Of Tampico, *Palmer 487,* May 1–22 1910 (GH, K,

NY);—Mcpo. Victoria, vic. Of Victoria, *Palmer 221,* 1 Feb to 9 Apr 1907 (GH, K, NY, US); vic. Of Victoria, *Palmer 515,* May 1 to Jun 13, 1907 (GH, US); Veracruz,—Mcpo. Chalcaltianguis, Las Robles, Coasmalopam, *R. Hernandez, Trigos, & Trigos 1074,* May 1971 (GH);—Mcpo. Emiliano Zapata, Plan del Río, *Ventura 3012,* 21 Jan 1971 (NY);—Mcpo. Huatusco, A few miles NE of Huatusco, *Barr & Dennis 64-267,* 13 Jun 1964 (ARIZ); —Mcpo. Hueyapan de Ocampo, Zacuapan and vic., *Purpus 2064,* Jun 1906 (BM, GH, NY, US);— Mcpo. Jalapa, near Jalapa, *Pringle 7823,* 1 Apr 1899 (US);—Mcpo. Misantla, Independencia, *Ventura 985,* 27 Apr 1970 (ARIZ);—Mcpo. Pueblo Viejo, 5 km S. of Mata Redonda, *Nevling & Gomez-Pompa 453,* Sep 1967 (GH);—Mcpo. Tampico Alto, 30–35 km S. of Mata Redonda, *Nevling & Gomez-Pompa 467,* Sep 1967 (GH);—Undetermined localities in Veracruz, Region d' Orizaba, *Bourgeau 2438,* 24 May 1865–1866 (GH); Mirador, *Purpus 8805,* Jun 1921 (UC, US); Quintana Roo,—Mcpo. José María Morelos, Chichankanab, *Gaumer 1784,* no date (NY); Chichankanab, *Gaumer 1889,* no date (GH); Undetermined locality in Mexico, Valle de Cordova, *Bourgeau 2336,* 4 May, 1865–1866 (GH); USA: Texas,—Webb Co., Laredo, Water St., 4 blocks E. of International Bridge, *Dickey 6,* 3 Nov 1962 (FSU).

Passiflora foetida var. maxonii

MÉXICO: Chiapas;—Mcpo. Chiapa de Corzo, between Chiapa de Corso and Río Guijava, *Carlson 2035,* 4 May 1949 (NY); Michoacan,—Mcpo. Coalcomán, Coalcomán, *Hinton 15939,* 1 Aug 1941 (NY).

Passiflora foetida var. nicaraguensis

MÉXICO: Tabasco,—Mcpo. Centla, 43.6 km de Villahermosa a Frontera, *Gleissman & McGalpin 1702,* 5 Nov 1978 (NY);—Mcpo. Cunduacan, Los Mulatos, *Ventura 20093,* 23 Mar 1983 (NY);— Mcpo. Paraiso, Barra de Tupilco, *Cowan & Magaña 2110,* 5 Jun 1979 (NY); Veracruz,—Mcpo. Tlacotalpan, waterfront along Río Palaloapan, *Nee & Taylor 26725,* 23 Apr 1983 (NY); Yucatan,— Mcpo. Telchac Puerto, 15 km from O de Telchac Puerto, *Cabrera 10249,* 24 Dec 1985 (NY); NICARAGUA: Dpto. Grenada, Grenada, *Baker 74,* 11 Feb 1903 (ROCH).

Passiflora foetida var. nigelliflora

ARGENTINA: Catamarca,—Mcpo. La Paz, Milocho, *Brizuela 1247,* 26 Feb 1947 (K); Portillo Chico, *Brizuela 694,* 5 Feb 1950 (GH); Cordoba,— Mcpo. Alta Gracia, Cumbre Chica, *King 611,* 30 Mar 1930 (BM);—Mcpo. Calamuihita, Portero de Lujan, *Galander s.n.,* 25 Jul 1883 (NY);—Mcpo. Pemilla, El Durazno, *Rodrigo 563,* Feb 1936 (NY); El Durazno, *O'Donell & Rodriguez 848,* 18 Mar 1944 (GH);—Mcpo. Totoral, Sierra Chica (Falda

O), Cerro Uritorco, *Hunziker 8514,* 19 Jun 1950 (NY);—Undetermined localities in Cordoba, *Lossen 312,* 25 Mar (GH); Entre Río de la Poblacion y Río de la Puerta, *Hieronymus s.n.,* 30 Mar 1879 (NY); around La Falda, *Job 494,* Jan 1936 (GH); Formosa,—Mcpo. Matacos, 23 km S. of Ing. *Juarez et al. 46385,* 26 Nov 1994 (GH, K); La Ríoja,— Mcpo. Fauvativa, Guanchin, *Venturi 7794,* 23 Dec 1928 (GH, K); Misiones,—Mcpo. Candelaria, costas del Río Paraná, *Bertoni 2652,* 18 Jan 1946 (K); —Mcpo. San Ignacio, Escala, *Montes 1935,* 16 Feb 1946 (K); Salta,—Mcpo. Candelaria, *O'Donell 4343,* 28 Jan 1947 (K); San Luis, Merlo, Piedra Blanca, *Burkart 13930,* 27 Jan 1944 (GH); Santiago del Estero,—Mcpo. Capital, Río Dulce, Santiago del Estero, *Tweedie 1171,* no date (K);—Mcpo. Jimenez, Munti Flor, *Luna 7,* 29 Jul 1946 (NY);— Undetermined locality in Santiago del Estero, Camino de Las Fermas a Santiago, *Diaz 110273,* 7 Nov 1944 (GH); Tucuman,—Mcpo. Leales, Leales, *Venturi 625,* Nov 1919 (GH);—Mcpo. Burrayaco, El Cajon, *Venturi 10338,* 16 Mar 1930 (GH);—Undetermined locality in Tucuman, *Roth s.n.,* no date (NY); PARAGUAY: Central, Estero del Ypoá, 18 km S of Puerto Guyrati, *Zardini & Tilleria 35423,* 4 Mar 1993 (NY); San Pedro, Alto Paraguay, Chaco, *Fiebrig 1235,* 1906 (K); Undetermined localities in Paraguay, Gran Chaco, *A. Pride s.n.,* no date (K); Cerro Geron, *Balansa 2206,* 1877 (K [isotype of *P. foetida* var. *balansae* Chodat]); Gran Chaco, Loma Clavel, *Hassler 2627,* Nov 1903 (BM, GH, K, NY); URUGUAY: Banda Oriental, *Tweedie s.n.,* no date (K).

Passiflora foetida var. oaxacana

MÉXICO: Oaxaca,—Distr. Tehuantepec, Tehuantepec, *Deam s.n.,* 23 Dec 1898 (GH); 4 km NNE of Tehuantepec, *King 1323,* 5 Jul 1959 (NY, US);—Distr. Juchitan, 50 mi W. of Tapanatepec, *Dunn, LeDoux, & Wallace 21923,* 4 Aug 1965 (NY);—Distr. San Mateo del Mar, Huazantlan del Río, *Zizumbo & Colunga 72,* 12 Jan 1973 (UC);— Distr. Pochutla, Puerto Angel, *Morton & Makrinius 2616, 12 Apr 1933* (K, US);—Undetermined localities in Oaxaca, San Geronimo, *Nelson 2762,* 1–5 Jul 1895 (GH, US [holotype]); Picacho, *Purpus 7145,* Jul 1914 (BM); plain of Tehuantepec, *Alexander 100,* 20 Dec 1944 (NY).

Passiflora foetida var. parvifolia

MÉXICO: Guerrero,—Mcpo. Acapulco, Acapulco and vicinity, *Palmer 315,* Oct 1894 to Mar1895 (GH, US [holotype]); N. Acapulco, *Clark 7165,* 23 Jun 1935 (NY); Jalisco,—Mcpo. La Huerta, Rancho Cuixmala, *Lott 4154,* 5 Nov 1991 (NY);—Undetermined locality in Jalisco, Puerto los Mazos, *Walker s.n.,* 4 Aug 1968 (K, NY).

Passiflora foetida var. salvadorensis

NICARAGUA:—Dpto. Managua, 12 km E. of Managua, *Atwood 5444,* 6 & 8 Apr 1971 (UC).

Passiflora foetida var. subpalmata

MÉXICO: Oaxaca,—undetermined locality, Tosolapam, *Seler 1670,* 4 Jan 1896 (GH, K, NY); Yucatan,—Mcpo. Progreso, Progreso, *Steere 3021,* 11–15 Aug 1932 (US); Progreso, *Steere 3022,* 11–15 Aug 1932 (US [holotype]);—Mcpo. Tinum, Chichen Itza, *Lundell & Lundell 7314,* Jun–Jul 1938 (US);—Undetermined locality in Yucatan, km 10, Meridia-Progresso road, *Lundell & Lundell 8123,* May–Aug 1938 (US); Undetermined localities in Mexico, *Gaumer 3979,* 1917–1921 (US); *Gaumer 24251,* 1917–1921 (GH, US).

Passiflora foetida var. tepicana

MÉXICO: Nayarit,—Mcpo. San Blas, San Blas, Tepic, *Nelson 4351,* Jun 1897 (GH, US);—Mcpo. Acaponeta, Between Pedro Paulo and Sam Blascito, *Rose 1998,* 4 Aug 1897 (GH, US [holotype]).

Passiflora foetida var. vitacea

ARGENTINA: Chaco, Urien, *Schulz 821,* 5 Dec 1945 (K); Corrientes,—Mcpo. General Paz, Los Cubanos, *Schwarz 280,* 12 Apr 1944 (GH, NY);—Mcpo. San Miguel, *Ibarrola 4079,* 15 Jan 1946 (NY); Chaco, Las Palmas, *Jorgensen 2616,* Nov 1917 (GH); Misiones,—Mcpo. Apostoles, Apostoles (Puebla legua al Oeste), *Ibarrola1098,* Nov 1944 (GH); Tucuman,—Mcpo. Burrayaco, El Puestito, *Venturi 7504,* 14 Nov 1928 (GH); Bolivia, Chiquitos,—Mcpo. Santa Cruz, 2–4 km ESE of Santiago, *Daly et al. 6303,* 22 Nov 1989 (NY); PARAGUAY: Cordillire de Peribobuy, *Balansa 2207,* 20 Dec 1875 (K); Canendiyu, Sierra de Maracayu, Yerbales, in regione fluminis Tapiraguay, *Hassler 4329,* Aug 1900 (BM, K, NY); Sierra de Maracayu, Yerbales, in regione fluminis Capibary; *Hassler 5934,* Dec 1900 (BM, K, NY; isotypes *P. chrysophylla* var. *hastata* Chodat); In regione cordillerae centralis, *Hassler 7132,* 1900 (BM); Caaguazu, in regione fluminis Yhu, *Hassler 9562,* Oct 1907 (BM, K, NY).

Passiflora foetida Unassigned Variety

MÉXICO: Yucatan,—Mcpo. Tinum, Chichen Itza, *Lundell & Lundell 7314,* Jun–Jul 1938 (GH) [possibly a hybrid of small size between var. *ciliata* and var. *mayarum*]; CULTIVATED MATERIAL: Cultivated at Cornell University, originally from Goulds, Dade Co., Florida, *Goldman 1768,* 6 Jul 2001 (BH) [possibly var. *ciliata* (Dryand.) Mast., or var. *riparia* (C. Wright) Killip]; as in *Goldman 1768, Goldman 1773*; 17 Jun 2001 (BH); as in *Goldman 1768, Goldman 2158*; 27 Oct 2001 (BH); Cultivated at Cornell University, seed source unknown, *Goldman 1793,* 4 Aug 2001 [probably a pubescent version of the plant represented in *Goldman 1768, 1773, 2158*].

Passiflora fruticosa

MÉXICO: Baja California Sur,—Mcpo. Comondú, Magdalena Island, *Brandegee s.n.,* 1 Mar 1889 (US); Magdalena Island, *Brandegee s.n.,* 11 Mar 1889 (UC); Magdalena Island, *Brandegee s.n.,* 12 Mar 1889 (GH); Santa Margarita Island, *Rose 16285,* 20 Mar 1911 (NY, US [holotype, #638347]); Magdalena Island, *Orcutt 70,* Mar 1917 (US); Revillagegido Islands, Magdalena Bay, *Mason 1919,* 29 May 1925 (GH, K, US); Bahía Magdalena, *Solis s.n.,* 30 May 1925 (US); W. Side of Santa Cruz Island, *Moran 3828,* 13 Apr 1952 (UC); middle of W. side of Catalina Island, *Moran 9349,* 9 Apr 1962 (NY);—Mcpo. La Paz, Espiritu Santo, *Brandegee s.n.,* no date (GH); Espiritu Santo Island, *Bryant s.n.,* no date (UC); Magdalena Bay, *Brandegee 4719,* 14 Jun 1889 (NY); La Paz, *Nuñez s.n.,* 18 Aug 1919 (US); San Francisco Island, *Johnston 3951,* 30 May 1921 (US); Espiritu Santo Island, *Johnston 3978,* 31 May 1921 (US); San Francisco Island, *Collins et al. 188,* 2 Apr 1931 (US); San Francisco Island, *Moran 3712,* 10 Apr 1952 (UC); W. shore of Isla San Francisco, *Wiggins et al. 384,* 7 Dec 1959 (UC); Isla San Francisco, *Wiggins 17682,* 13 Apr 1962 (US); San Diego Island, *Moran 9581,* 19 Apr 1962 (BH, GH, UC); 5 mi NW of La Paz, *Taylor & Taylor 15731,* 28 Mar 1974 (NY); Isla Espiritu Santo, *Tenorio 11810,* 6 Aug 1986 (ARIZ);—Mcpo. Mulegé, 25 mi W. of Santa Rosalia, *Chambers 772,* 3 Aug 1955 (UC); Undetermined localities in Mexico: *Brandegee s.n.,* 1889 (US); Bahía San Francisco, *Russell & Maya s.n.,* 30 Jul 1962 (ARIZ).

Passiflora palmeri var. palmeri

MÉXICO: Baja California,—Mcpo. Ensenada, Angel de la Guarda Island, *Johnston 3397,* 2 May 1921 (GH, K, US); Isla Angel de la Guarda, *Johnston 3406,* 3 May 1921 (GH, NY, US); Las Animas Bay, *Johnston 3500,* 8 May 1921 (GH, K, NY, US); South San Lorenzo Island, *Johnston 3536,* 9 May 1921 (GH, K, US); Pt. San Fermin, *Harvey 646,* 24 Apr 1933 (US); 10.5 km W. of Mision San Gertrudis, *Carter & Kellogg 2958,* 18 Dec 1950 (GH, K, UC, US); Angel de la Guarda Island, Refugio Bay, *Moran 4098,* 9 May 1952 (BH); Bahía San Francisquito, *Russell & Maya s.n.,* 30 Jul 1962 (ARIZ); ca. 27 mi S. of Bahía de Los Angeles, in Arroyo Venacas, *Henrickson 1132,* 28 Feb 1963 (GH); El Barril, 20 mi N. of Baja California Sur border, *Felger et al. 6484,* 9 Mar 1963 (ARIZ); Isla Angel de la Guarda, *Hastings 71-24,* 14 Mar 1971 (ARIZ); Isla Angel de la Guarda, *Valiente & Chiang 593,* 4 Aug 1985 (ARIZ); Isla Angel de la Guarda, *Tenorio & Romero 10953,* 18 Feb 1986 (US);—Mcpo. Mexicali, 60 mi N. of San Felipe, *Weeks s.n.,* 27 Oct 1950 (UC); 2 mi N. of La Ventana, *Johnston*

s.n., 6 Mar 1953 (GH); 2.1 mi S. of La Ventana, *Wiggins 13024,* 6 Apr 1954 (GH, UC); 8 mi S. of La Ventana, near hwy between Mexicali and San Filipe, *Wiggins & Wiggins 15772,* 17 Mar 1960 (GH, K, US); 16.5 mi N. of junction of Mexico 3 and Mexico 5, *Bowers & McLaughlin 1975,* 9 May 1980 (ARIZ);—Undetermined locality in Baja California, Puertecitos, *Moran 12882,* 23 Mar 1966 (ARIZ); Baja California Sur,—Mcpo. Comondú, Carmen Island, *Palmer 868,* 1–7 Nov, 1890 (GH, K, NY, US [holotype, #46866]); Carmen Island, *Rose 16615,* 2 Apr 1911 (US); head of Concepcion Bay, *Rose 16691,* 6 Apr 1911 (NY, US); San Nicholas Bay, *Johnston 3721,* 16 May 1921 (GH, K, UC, US); Coronados Island, *Johnston 3759,* 18 May 1921 (US); Isla Carmen, wash at Puerto Balandra, *Johnston 3823,* 22 May 1921 (GH, K, NY, US); Agua Verde Bay, *Johnston 3882,* 26 May 1921 (GH, K, UC, US); Agua Verde Bay, *Collins et al. 234,* 3 Apr 1931 (GH, US); Shore of Bahía Concepcion, between Mulege and head of bay, *Wiggins 5451,* 24 Apr 1931 (BH, GH, NY, UC, US); west cove in Bahía Concepcion, *Rempel 175,* 15 Mar 1937 (ARIZ); rocky arroyo inland from Concepcion Bay, just W. of Coyote Cove, *Hammerly 424,* 25 Oct 1941 (GH, US); Foothills of the Sierra de la Giganta, W. of Loreto, *Carter & Kellogg 3154,* 11 Oct 1951 (ARIZ, UC, US); Isla Carmen, Puerto Balandra, *Carter & Ferris 3745,* 11 Mar 1960 (BM, GH, UC); Isla Coronado, *Carter 4327,* 25 Nov 1961 (UC); near S. end of Isla Coronado, *Wiggins 17462,* 3 Apr 1962 (US); Danzante Island, *Moran 9223,* 7 Apr 1962 (US); Bahía de la Concepcion, at Santispaquis, *Wiggins & Wiggins 17977,* 18 Oct 1962 (US); in Canyon E. of Punta Santo Domingo, Bahía de la Concepcion, *Wiggins & Wiggins 18113,* 21 Oct 1962 (US); Isla Carmen, *Carter & Reese 4547,* 4 Jun 1963 (ARIZ, UC); Isla Carmen, Puerto Ballandra, *Hastings 71-129,* 1971 (ARIZ); Bahía Concepcion, 3 mi NW of Isla Requeson turnoff, *Webster 19608,* 23 Mar 1974 (GH); 8 km W. of Loreto, *Fuerte 188,* 13 May 1984 (UC); Agua Grande, Isla El Carmen, *Tenorio 11845,* 10 Aug 1986 (ARIZ); Playas Santispac, N. end of Bahía Concepcion, *Van Devender & Van Devender 91-455,* 16 Mar 1991 (ARIZ); 2 k W. of Bahía Concepcion, 6 mi SE of Estero Mulege, *Baker & Johnson 8720,* 29 Feb 1992 (ARIZ);—Mcpo. La Paz, Ceralbo Island, Ruffo's Ranch, *Johnston 4043,* 7 Jun 1921 (GH); San Francisco Island, *Moran 3712,* 10 Apr 1952 (BH); 3 mi N. of El Coyote, *Thomas 7967,* 24 May 1959 (US); W. shore of Isla San Francisco, *Wiggin et al. 384,* 7 Dec 1959 (US); Sierra de la Giganta, near Rancho San Bernardo, N. of Bahía Agua Verde, *Carter & Sharsmith 4939,* 4 Jun 1965 (ARIZ, GH); 1.6 mi S. of Rancho El Coyote turnoff via Hwy 1, *Burgess et al. 6124,* 15 Oct 1981 (ARIZ); Sierra de la Giganta, along trail from San Jose de Agua Verde to Bahía Agua Verde, *Carter 5977,* 31 May 1983 (UC);—Mcpo. Mulegé, San Marcos Island, *Johnston 3640,* 12 May 1921

(GH, US); Mulegé, *Johnston 3659,* 13 May 1921 (US); 5 mi N. of Santa Rosalia, *Gentry 3685,* 15 Apr 1938 (ARIZ); 12 mi S. of Mulege on Mex 1, *Lynch 1111,* 23 Mar 1975 (NY); S. of Santa Rosalia, *Spjut & Marin 6047,* 27 Mar 1980 (US);—Undetermined localities in Baja California Sur, About half way between Mulegé and El Coyote, *Thomas 7969,* 24 May 1959 (ARIZ, BM, US); Mainland at Bahía Trinidad, *Hastings 71-93,* 21 Mar 1971 (ARIZ); Sonora,—Mcpo. Hermosillo, San Esteban Island, *Johnston 3167,* 19 Apr 1971 (GH, K, US); S. shore of Isla Tiburón, Ensenada de la Cruz, *Felger & Howe 2588 & 1788,* 8 Apr 1958 (ARIZ); NE side of Turner's Island (Isla Dátil), *Felger 9099,* 21 Oct 1963 (ARIZ); S. side of Tiburón Island, *Felger et al. 10095,* 15 Jul 1964 (ARIZ); NE side of Turner's Island, *Felger & Soule 13451,* 4 Dec 1965 (ARIZ); Isla Dátil, *Felger & Cooper 15315,* 20 Dec 1966 (ARIZ); Tiburón Island, Tordillitos, *Felger & Cooper 15485,* 22 Dec 1966 (ARIZ); Ensenada Blanca, *Felger et al. 15734,* 28 Apr 1967 (ARIZ); Tiburón Island, Ensenada Blanca, *Felger et al. 17267,* 20 Feb 1968 (ARIZ); Tiburón Island, Ensenada de la Perra, *Felger et al. 17710,* 12 Apr 1968 (ARIZ); Isla Tiburón, *Wilkinson 216,* 11 Oct 1977 (ARIZ); Bahía Agua Dulce, Punta Norte de la Isla Tiburón, *Tenorio 9535,* 11 Aug 1985 (US); S. side of Tiburón Island, Sau Sal drainage, *Tewksberry et al. s.n.,* 1 Aug 1992 (ARIZ).

Passiflora santiagana

CUBA:—Santiago de Cuba, vic. of El Morro, Santiago Bay, *Britton & Cowell 12546,* 10–11 Mar 1912 (GH); vic. of Santiago city, *Pollard et al. 279,* 14 Feb 1902 (BH, GH [isotypes]); Camino Viejo del Morro, Clemente 2341, 10 Feb 1938 (GH); Renté, *Clemente 2576,* Jan 1943 (GH); Renté, Santiago, *Clemente 2629,* Apr 1943 (GH); Renté, Santiago, *Clemente 2719,* May 1943 (GH); Sardinero, *Clemente 6447,* Feb 1949 (GH); Renté, Santiago, *Clemente 6504,* Mar 1949 (GH).—Undetermined locality in Cuba, *Linden 1703,* 1843–1844 (K).

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FLOOD TOLERANCE OF THE THREATENED
SIDALCEA NELSONIANA (MALVACEAE)

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Abstract

Sidalcea nelsoniana (Nelson's checkermallow) is a federally threatened plant native to wetlands of the Willamette Valley, Oregon, USA. Wise conservation and management of this species requires an understanding of its hydrologic tolerance. Because of extreme habitat loss, the current distribution of this species might not reflect the full range of suitable habitats. The purpose of this study was to test the effect of flooding on *S. nelsoniana* survival and vigor. Rhizome fragments collected from mature individuals were transplanted into 32 15-cm pots exposed to four artificially maintained flooding conditions: drained soil, saturated soil with no standing water, standing water mid-November through mid-April, and standing water mid-November through mid-June. All plants with drained soil died as the spring rains declined, and all plants flooded past April died by mid-June. Plants in saturated soils and those flooded until mid-April were most successful and similar in survival; number, height, and cover of leaves; and number and height of flowering stems. These two treatments most closely match conditions now found in Willamette Valley wetland prairies, suggesting that the current distribution of *S. nelsoniana* does reflect its hydrologic tolerance. Management recommendations to flood a population of *S. nelsoniana* beyond mid-April are likely to harm this protected species.

Key Words: flooding tolerance, habitat management, hydrology, rare plant, *Sidalcea nelsoniana*, wetlands.

With the rapid decline in wetland habitat that has occurred over the past 150 years in North America, proper management of existing habitat and restoration of degraded areas is crucial to the preservation of these resources. Because hydrologic regime, especially duration of flooding, plays a key role in determining wetland vegetation (Lippert and Jameson 1964; van der Valk 1981; Nelson and Anderson 1983; Welling et al. 1988; Trebino et al. 1996), wetland management and restoration must maintain a suitable water regime. Additionally, many rare plants in wetlands have specific hydrologic requirements (Harvey and Meredith 1981; Lesica 1992; Davis 1993). Therefore, effective conservation management requires an understanding of the response of plant species to current and proposed hydrologic conditions. Often descriptive studies are inadequate for this purpose because past habitat destruction can lead to current distributions that are restricted to sites with suboptimal environmental conditions. This study tests the tolerance of a protected rare plant to experimentally manipulated patterns of flooding, including a proposed increase in flooding duration.

Sidalcea nelsoniana Piper (Malvaceae) (Nelson's checker-mallow) is a perennial herb native to wetland prairies and streamsides of the Willamette Valley, Oregon, some adjacent areas of the Oregon Coast Range, and a site in Cowlitz County, Wash-

ington (U.S. Fish and Wildlife Service 1993). Land use changes over the past 150 years have altered or destroyed more than 99% of wetland habitats in the Willamette Valley and limit the current distribution of *S. nelsoniana* to just 64 sites, many with fewer than 100 plants (U.S. Fish and Wildlife Service 1998). Remaining populations are threatened by encroachment of woody species, road management activities, and continuing agricultural and commercial development. As a result, *S. nelsoniana* is listed under the federal Endangered Species Act as threatened with extinction (U.S. Fish and Wildlife Service 1993). It is also listed as threatened by the State of Oregon (State of Oregon 1995).

The threatened status of *S. nelsoniana* has prompted interest in expanding current populations or re-establishing new populations. For example, managers of the William L. Finley National Wildlife Refuge near Corvallis, Oregon, which contains the largest numbers of *S. nelsoniana,* have proposed an increase in flooding duration of six to eight weeks into the spring and early summer (James Houk, U.S. Fish and Wildlife Service personal communication). Unfortunately, there are no experimental data on the hydrologic tolerance of *S. nelsoniana,* and because of dramatic habitat loss, the current distribution of this species offers limited insight into its true hydrologic tolerance. As a result, it is difficult to predict how extended inundation would affect this protected species.

This experimental study was designed to evaluate the flooding tolerance of *S. nelsoniana* and to predict the effect of increased flooding duration on the vigor of *S. nelsoniana* grown from rhizome

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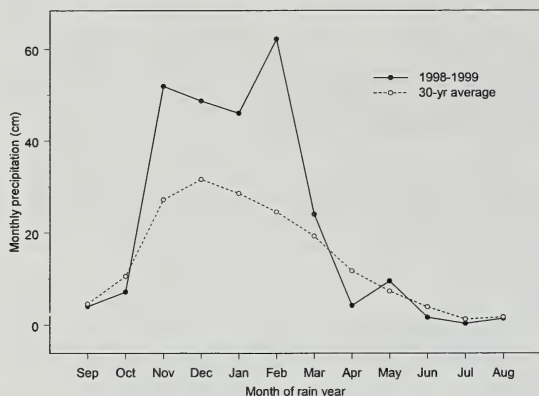
Fig. 1. Monthly precipitation from September 1998 to August 1999 at the Corvallis Water Bureau, 14 km northeast of the study area, and 30-year averages from 1971 to 2000.

fragments. The study tested hypotheses about survival and growth: Increased duration of flooding will lower shoot survival and growth of *S. nelsoniana* because prolonged inundation rots rhizomes or because anaerobic respiration and diminished photosynthesis of submerged leaves are inadequate; alternatively, extended duration of flooding will promote *S. nelsoniana* survival and growth because the growing season will be shifted to a warmer, more productive time of year.

METHODS

Sidalcea nelsoniana is a gynodioecious species that can propagate from either rhizomes or seeds. It is most often found in wetland prairies, streamsides, ash swales, and roadside ditches. Peak flowering occurs mid-June through mid-July in the Willamette Valley, with fruits maturing in late July and early August (U.S. Fish and Wildlife Service 1993).

The study was located approximately 500 m from a large *S. nelsoniana* population at William L. Finley National Wildlife Refuge (NWR), 16 km south of Corvallis, Oregon, USA (123°19′W, 44°24′N). This location was chosen to closely match natural growing conditions of temperature, photoperiod, and precipitation. The region experiences a modified maritime climate, with cool, wet winters and warm, dry summers. Average annual precipitation as recorded in Corvallis is 108.5 cm, with 93.0 cm occurring October through April (Fig. 1). Mean monthly temperatures range from a minimum of 0.6°C in January to a maximum of 26.8°C in July (Oregon Climate Service 2002).

Rhizome fragments were used as the propagules in this experiment because of their success in other transplant experiments (CH2M Hill 1986, 1987) and because they are more likely to simulate the response of mature individuals. During October 1998, rhizome fragments were collected from dor-

mant *S. nelsoniana* individuals that had been marked during the previous growing season. Eighteen fragments were collected from six plants from Finley NWR and 22 fragments were collected from six plants near Oregon State University.

Rhizomes were given a unique identification code and weighed before transplanting. Fragments larger than 7.5 g were cut into smaller pieces and re-weighed. Of those fragments weighing between 3.0 and 7.0 g, sixteen from each of the two populations were randomly selected for use in the experimental study, for a total of 32 experimental units. Each rhizome fragment was transplanted into a 15-cm pot filled with 10 cm of native wetland soil similar to that found at many *S. nelsoniana* sites (a silty clay loam collected from Finley NWR). Rhizomes were planted at a depth of 2 cm to 3 cm below the soil surface. Transplanted rhizomes were stored in a temperature-controlled greenhouse for up to two weeks before experimental conditions were applied.

Potted rhizome fragments from each of the source populations were randomly assigned to one of the four flooding treatments, yielding eight replicates of each treatment. Pots were transported to Finley NWR on November 10, 1998 and randomly arranged within a 122 cm diameter by 30 cm deep plastic wading pool. Treatments were applied as follows:

· Drained soil (*Dr*): Pots were elevated above the surface of the water on concrete blocks.
· Saturated Soil (*SS*): Pots were placed on concrete blocks so that the water level was approximately at the soil surface from November 20, 1998 through April 15, 1999. After April 15, the pots were elevated above the water surface and allowed to drain.
· Flooded until April (*FA*): Pots were placed on the bottom of the pool until April 15, 1999 and then elevated above the water surface on concrete blocks.
· Flooded until June (*FJ*): Pots were placed on the bottom of the pool until June 23, 1999 and then elevated above the water surface on concrete blocks.

Saturated soil with no standing water (*SS*) and flooded from mid-November until mid-April (*FA*) are the treatments that most closely match the range of hydrologic conditions in which *S. nelsoniana* is currently found.

To maintain a relatively constant water level, the pool was filled with water so that excess precipitation flowed over the edge, resulting in 20 cm of water above pots on the bottom of the pool (*FA* and *FJ* treatments). The pool was monitored throughout the winter and there was no sign of harm due to algal or microbial growth. All pots were top watered every two weeks between June 10 and July 14, 1999. Pots were weeded and rotated 90 degrees at the time of each measurement. Pots

were randomly re-arranged within the pool on April 15 and June 23, 1999.

The number of leaves and the height of the tallest leaf was recorded for each pot every two to four weeks from November 10, 1998 through July 14, 1999. All basal and cauline leaves were included in the leaf count. Leaf height was measured to the junction of the blade and the petiole on the tallest fully emerged leaf. Survival was recorded as the persistence of green leaves above the soil surface. Number and height of flowering stems were also recorded when present. Absolute leaf area was estimated for each surviving individual on July 14, 1999 using calibration templates.

Plant characteristics as recorded on July 13–14, 1999 were analyzed using a multi-factor analysis of variance (ANOVA, Statgraphics Plus for Windows 4.0). A separate ANOVA was performed for each of the growth characteristics measured (leaf height, number of leaves, leaf area, stem height and number of stems). Main effects were treatment and source population. Because population and population × treatment interaction were never significant factors, their sums of squares were added to the residual sums of squares. Height and number of leaves as recorded November 10, 1998 (before treatments were applied) were used as covariates in their respective analyses. Rhizome weight was used as a covariate in the analyses of leaf area and flowering characteristics. Rhizome fragments that did not emerge over the course of the study were assumed to be non-viable and were excluded from the analyses. Means were adjusted for initial size (the covariate).

FIG. 2. Survival and vigor of *Sidalcea nelsoniana* rhizome fragments exposed to altered flooding regimes. See Methods for details of treatments. (a) Survival as a proportion of maximum number emerged. (b) Mean maximum leaf height of surviving individuals. (c) Mean number of emerged leaves per surviving individual. Error bars = ±1 SE.

RESULTS

When potted rhizomes were transported to the experimental pool on November 10, 1998, leaves had emerged in all but three pots. Survival remained constant through the winter for the *SS* (saturated soil), *FA* (flooded until April), and *FJ* (flooded until June) treatments but declined slightly for the *Dr* (drained soil) treatment (Fig. 2a). By mid-May, there were no surviving individuals in the *Dr* treatment. Survival in the *FJ* treatment declined sharply after mid-May, with only one individual surviving to June 10 and no individuals surviving to June 23. Survival in the *FA* treatment held steady at seven individuals until mid-April and then declined to six individuals for the duration of the study. All eight *SS* individuals survived for the duration of the experiment.

Maximum leaf height of surviving individuals in the *FA* and *FJ* treatments increased gradually from ~5 cm in November to ~10 cm by mid-April (Fig. 2b). Leaf heights of the *Dr* and *SS* treatments remained relatively low until mid-April. After mid-May, plants in the *SS* and *FA* treatments increased rapidly in height, reaching 31.0 ± 1.5 cm (least square mean ± standard error) for the *SS* treatment

and 43.2 ± 1.6 cm for the *FA* treatment. Leaf height in the *FJ* treatment declined slightly after mid-April, due to some mortality, and then remained steady until no surviving individuals remained. No individuals in the *Dr* treatment survived past mid-April.

Number of leaves on surviving individuals in the *SS*, *FA*, and *FJ* treatments remained similar throughout the winter (Fig. 2c). The average number of leaves in the *Dr* treatment declined sharply between mid-December and mid-January and remained lower than the other three treatments until there were no longer any surviving individuals. The number of leaves in both the *SS* and *FA* treatments continued to increase gradually after mid-April to 11.2 ± 1.2 for the *SS* treatment and 13.0 ± 1.3 for the *FA* treatment. The number of leaves declined steadily in the *FJ* treatment after mid-April until all individuals died. Average final leaf area was 92.5 ± 20.9 cm^2 for surviving plants in the *FA* treatment and 61.0 ± 17.0 cm^2 for surviving plants in the *SS* treatment.

Only those individuals in the *SS* and *FA* treatments produced flowering stems. Flowering stems first appeared on the May 27, 1999 sampling date and no new stems were produced after the June 23 sampling date. Five of six surviving individuals in the *FA* treatment produced flowering stems, averaging 1.2 ± 0.3 stems per individual. Five of eight individuals in the *SS* treatment produced flowering stems, averaging 0.8 ± 0.3 stems per individual. Of those plants that produced flowering stems, the average heights were 59.4 ± 11.9 cm for the *SS* treatment and 69.2 ± 10.1 cm for the *FA* treatment.

Pre-treatment size (the covariate) was positively related to final size: b = +1.4, P = 0.03 for leaf height; b = +1.7, P = 0.02 for number of leaves; b = +15.1, P = 0.14 for leaf area; b = +0.2, P = 0.07 for number of flowering stems; b = +4.7, P = 0.02 for height of flowering stems.

Plants in the *SS* and *FA* treatments did not significantly differ in their final maximum leaf heights, number of leaves, leaf area, number of flowering stems, and stem heights (all P > 0.21).

Discussion

Evaluation of Hypotheses

Decreased survival in the *FJ* treatment is consistent with the hypothesis that prolonged flooding damaged *S. nelsoniana* rhizomes or led to inadequate metabolism. U.S. Fish and Wildlife Service regulations required that, at the end of the experiment, all plants were to be grown out under optimal conditions for return to the field. No plants that had died off in the experiments showed any sign of regrowth during these two months of observation, reinforcing the conclusion that rhizomes had become nonviable.

Changes in leaf morphology caused by flooding might also have contributed to low survival. In mid-May, *S. nelsoniana* plants in both the *FA* and *FJ* treatments had long petioles which placed leaf blades at or just below the water surface (Fig. 3a). In contrast, the leaf blades of the *SS* individuals were larger and had shorter petioles (Fig. 3b). Four weeks after they were released from flooding, the *FA* leaf morphology more closely resembled the broader leaf blades of the *SS* individuals, whereas the leaf blades of the surviving *FJ* individuals remained small with long petioles. Gas exchange and photosynthetic rates of these small leaves might have been insufficient to keep *FJ* plants alive past April as temperatures and respiration increased. Blom et al. (1990) found that, in those *Rumex* species that were deemed "flood tolerant," flooding stimulated petiole and stem elongation, and plants were more likely to survive prolonged and deep inundation if their leaves protruded above the water surface.

Plants in the *Dr* treatment showed two periods of leaf and plant death. The slight decline in survivorship and sharp decline in number of leaves produced during the early winter months in the *Dr* treatment were likely due to an unusually cold weather system that affected the Pacific Northwest between December 19 and 25, 1998. Temperatures remained below freezing for 96 hours (Oregon Climate Service 2002) and a layer of ice formed at the surface of the pool. While the pots in the *FA*, *FJ*, and even the *SS* treatments were insulated to some degree by the surrounding water, the elevated plants in the *Dr* treatment were exposed to the cold air. Those individuals in the *Dr* treatment that survived through the cold spell persisted into spring, and even showed a slight increase in number of leaves between late February and mid-April. However, survivorship decreased sharply in April, a decline likely caused by sharply lower precipitation (Fig. 1). The effects of extreme temperatures and drought on these experimental plants might not be indicative of field conditions since plants growing in the field would be surrounded by a greater volume of soil, which would increase both insulation from extreme temperatures and water holding capacity. Although water added to the *Dr* pots exceeded precipitation, additional watering throughout the spring might have increased survival.

Although the *SS* and *FA* treatments did not result in statistically significant differences in mean maximum leaf height or number of leaves, the *FA* treatment performed slightly better than the *SS* treatment in both attributes (Fig. 2b, c). *S. nelsoniana* individuals might not only tolerate but perhaps even benefit from a certain amount of flooding, and flooding might be harmful only if it persists into late spring. This diatonic pattern, optimal conditions flanked by reduced performance with too little or too much flooding, is common with wetland and many other plants (Mitsch and Gosselink 2000).

Ecological and Management Implications

Recovery of the threatened *S. nelsoniana* can be aided by re-introduction. Vegetative multiplication by rhizome cuttings is an effective propagation and reintroduction technique for *S. nelsoniana*. Positive and often statistically significant relationships between pre-treatment measures of plant size and post-treatment vigor in this study show that selection of vigorous source plants can improve the performance of plants re-introduced through cuttings.

Recovery of *S. nelsoniana* can also be aided by restoration of habitat, especially hydrologic regime. The performance of *S. nelsoniana* under the experimental flooding conditions of this study suggests that the current distribution of *S. nelsoniana* does approximately represent its range of hydrologic tolerance. Survival and vigor were greatest in the *SS* and *FA* treatments, both conditions that exist naturally at many *S. nelsoniana* sites (personal observations). These hydrologic patterns are also typical of wetland and riparian prairies throughout the Willamette Valley, where winter rains and clay soils
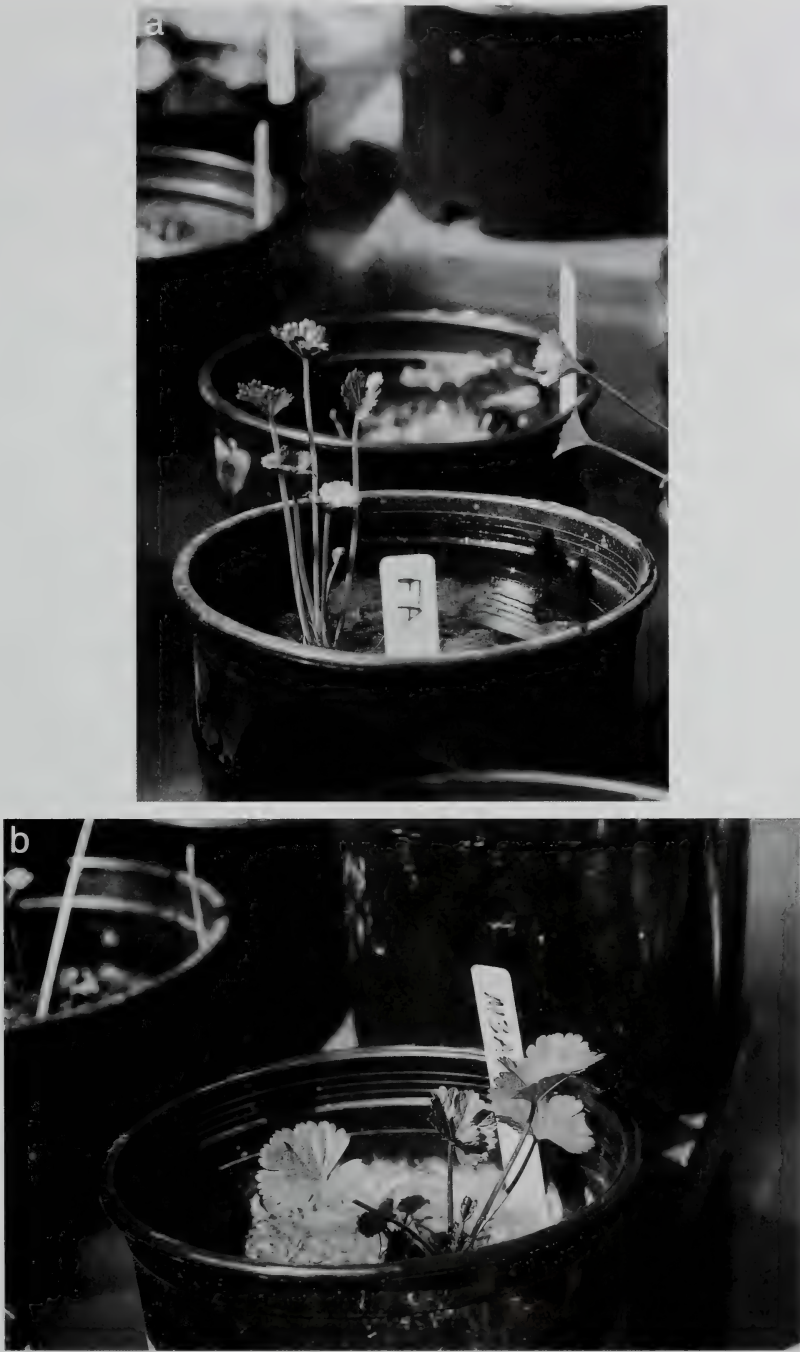
FIG. 3.   Leaf morphology of *SS* (saturated soil treatment) and *FA* (flooded mid-November until mid-April) individuals on April 15, 1999. (a) After being under 10 cm of water through the winter, the leaf blades of the *FA* individuals were small with long petioles. (b) In contrast, those plants that were not under water (*SS* treatment) had larger leaf blades and shorter petioles.

result in standing water and high water tables throughout the winter months. As precipitation decreases in the spring, these sites dry out and little or no standing water remains during the late spring and summer months (Finley 1995).

Low survival of plants in the *Dr* treatment shows the importance to *S. nelsoniana* reintroduction efforts of assuring adequate soil moisture, even during the normally rainy early growth season of late winter and early spring. In contrast, poor survival and vigor of plants flooded into June demonstrate that there is a limit to how much flooding this wetland species can tolerate.

While *S. nelsoniana* individuals might be able to survive some flooding beyond April, changing the flooding regime of a site can alter the entire plant community at that site (Harris and Marshall 1963; van der Valk 1981; Nelson and Anderson 1983; Moore and Keddy 1988). Such changes in the surrounding vegetation might affect *S. nelsoniana* indirectly by intensifying the competitive interactions with associated species. For example, prolonged flooding in wetland prairies of the Willamette Valley increases the likelihood or severity of encroachment by the pest plant *Phalaris arundinacea* (reed canarygrass), much in the way flooding promotes the pest plant *Typha domingensis* in the Florida Everglades (Newman et al. 1996).

Although there are obvious differences between this experimental study and *S. nelsoniana* field sites, these results suggest that inundating a *S. nelsoniana* site into June is likely to be detrimental to this rare species. Therefore, extreme caution should be exercised when managing for high water levels past mid-spring, the historical end of the flooding season in the Willamette Valley.

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ASSIGNING CLIMATE VALUES TO MODERN POLLEN SURFACE SAMPLE SITES AND VALIDATING MODERN ANALOG CLIMATE RECONSTRUCTIONS IN THE SOUTHERN CALIFORNIA REGION

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Abstract

In the modern analog technique (MAT), climate characteristics associated with the vegetation producing modern reference pollen assemblages are used to reconstruct the paleoclimates that occurred in association with vegetation producing similar (i.e., analogous) fossil pollen assemblages, based on the assumption that similarity of vegetation implies similarity of climate and other ecological characteristics. Quantitative reconstruction of paleoclimate using the MAT requires attribution of climate values at the modern reference pollen sites. In this paper, climate assignments for temperature and precipitation are determined for forty-one modern reference pollen sites in the southern California cismontane region. Six temperature lapse rates and eleven linear and non-linear equations fitted to precipitation-elevation relationships are used, based on instrumental data from available reporting stations in the region. The climate assignments match well with existing, less spatially-explicit, regional climate analyses and show ability to capture relatively small-scale variations of the region's climate patterns. The quality of the MAT when employed with the combined surface sample/climate data set is examined by reconstructing the modern climate and elevation at the surface sample sites. The general results of this validation analysis show that highly accurate, relatively precise temperature and apparent elevation reconstructions are achievable, while accurate, but somewhat less precise reconstructions of precipitation can typically be expected. When analog selection is largely confined to samples from montane conifer-dominated forests, high quality reconstructions of all the climate and elevation variables can be achieved.

Key Words: southern California, climate, climate reconstruction, paleoclimate, paleoecology, modern analog technique.

Pollen surface samples from lakes, bogs, small forest hollows, small clearings in vegetation, and moss polsters are commonly used as calibration sets to determine modern analogs for fossil pollen assemblages. Similar pollen spectra in modern and fossil samples are interpreted to imply that the vegetation, climate, and other ecosystem characteristics (e.g., forest structure and biomass) of the fossil site in the past were similar to those of its analog sites today (e.g., Maher 1972; Overpeck et al. 1985; Anderson et al. 1989; Anderson 1990; Guiot 1990; Bartlein and Whitlock 1993; Anderson and Smith 1994; Davis 1995; Davis et al. 1998, Peyron et al. 1998; Davis 1999; Davis et al. 2000; cf. Birks 1998 regarding use of modern analogs in European paleolimnology). This method of paleoecological reconstruction is commonly called the modern analog technique, or MAT.

Assigning climate values to surface sample sites in order to implement the MAT for quantitative climate reconstruction is often done using grids of interpolated climate data derived from instrumental records (e.g., Thompson et al. 1998; Bartlein et al. 1998; Minckley and Whitlock 2000). The resolu-tion of these data is typically on the order of 15–25 km per grid-square side. Site-specific estimates are determined using weighted averages of the nearest grid points, interpolated to the sites by using local lapse rates for elevation (Minckley and Whitlock 2000). Although this method is appropriate for use in many circumstances, it is coarse in relation to the fine-scale heterogeneity of environments in the Peninsular and Transverse Ranges of southern California (Wahl 2003). In these mountains, a horizontal distance of 15 km can encompass vertical distances of more than 2000 m, with large associated differences in climate, which makes averages of nearby grid points, even when downscaled using local lapse rates, an overly-smoothed tool. Finer-scale climate estimates have recently become available at 1 km² resolution (Daymet U.S. Data Center, University of Montana *http://www.daymet.org*); however, the period of the Daymet data, 1980–1997, determines that key observational records that could be exploited from the study region are not utilized in the construction of the Daymet estimates.* Climate estimates are developed here for the 41 modern pollen surface sample sites reported

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* For example, the data from the Mount San Jacinto WSP and Mill Creek 2 weather stations lie entirely out of the Daymet period of record (cf. Table 1); the Julian Wynola station record loses 19 out of its 28 years of coverage.

TABLE 1. WEATHER STATIONS USED TO ASSIGN CLIMATE VALUES TO SURFACE SAMPLE SITES. Normative Period of Record: 1961–1990. Stations with other periods of records: Escondido, 1961–1979; Escondido 2, 1980–1990; Julian Wynola, 1961–1988; Mill Creek 2, 1961–1967; Mount San Jacinto WSP, 1965–1978.

Station name	County	Latitude	Longitude	Elevation	COOPID #
Alpine	San Diego	32:50	−116:47	528.8	40136
Big Bear Lake	San Bernardino	34:15	−116:53	2069.6	40741
Cuyamaca	San Diego	32:59	−116:35	1414.3	42239
Descanso Ranger Stn	San Diego	32:51	−116:37	1066.8	42406
Escondido	San Diego	33:07	−117:05	200.9	42862
Escondido No 2	San Diego	33:07	−117:06	182.9	42863
Idyllwild Fire Dept	Riverside	33:45	−116:42	1639.8	44211
Julian Wynola	San Diego	33:06	−116:39	1112.5	44418
La Mesa	San Diego	32:46	−117:01	161.5	44735
Lake Arrowhead	San Bernardino	34:15	−117:11	1586.5	44671
Mill Creek 2	San Bernardino	34:05	−117:02	897.0	45629
Mount San Jacinto WSP	Riverside	33:48	−116:38	2567.9	45978
Palomar Mountain Observatory	San Diego	33:23	−116:50	1691.6	46657
Redlands	San Bernardino	34:03	−117:11	401.7	47306

in the companion paper (Wahl 2003), based on mountain-specific temperature lapse rates and linear/non-linear precipitation-elevation equations. These relationships are derived primarily from the available instrumental data in the region (U.S. Department of Commerce, National Oceanic and Atmospheric Administration—NOAA), with additional reference to interpolated precipitation isohyets developed by the U.S. Department of Agriculture (*California Annual Precipitation* map 1999).

In quantitative applications of the MAT, it is possible to rigorously test the reconstruction capabilities of the calibration set in order to validate its use in the MAT procedure (e.g., Overpeck et al. 1985; Guiot 1990; Bartlein and Whitlock 1993; Birks 1998; Davis et al. 2000; Seppä and Birks 2002). In this paper, the MAT is used with the climate values assigned to the surface sample sites to reconstruct each site's modern climate and elevation, based on analogy of pollen spectra, which provides a quantitative test of the likely ability of the surface sample set to be successful in reconstructing paleoclimates in the region. This test is necessarily indirect, but it is logically equivalent to known-data and historical-period goodness of fit tests used to gauge the likely success of prediction models in a variety of disciplines. A key assumption of this procedure is that the modern surface sample set contains potential analogs encompassing the range of vegetation types and climates likely to be encountered during the time period studied at the paleo-reconstruction sites where it is used. The validity of this assumption for the surface sample set examined here, and for its use in reconstructing Holocene vegetation and climate at fossil pollen sites in the cismontane region of the Peninsular and Transverse Ranges, is examined in Wahl (2003).

METHODS

Climate Assignments

The basic climate data set consists of instrumental weather records from all the reporting stations

in the NOAA database in the mountain and foothill areas of the study region, which is east of Los Angeles and San Diego (Table 1; Fig. 1 in Wahl 2003). These data were downloaded at *http://www5.ncdc. noaa.gov:7777/plclimprod/plsql/poemain.poe*. One station (La Mesa) nearer the Pacific Ocean coast was also used. The standard period of record is 1961–1990 (for both instrumental temperature/precipitation data and map-derived precipitation data); deviations from this period are noted in Table 1. The data were utilized as the mean during the period of record for each climate variable. Missing values in the record were estimated as the average of the five previous and five following values in the series. When a missing value was less than five years from the beginning or end of the series, the estimation included all values available between the missing value and the end of the series.

The primary method for assigning climate values to the surface samples developed mountain-specific lapse rates for temperature and linear/non-linear precipitation-elevation equations for precipitation; these relationships were applied to the surface sample sites based on their elevation. Six lapse rates each were determined for January and July temperature, and eleven equations were determined for annual precipitation. The extra relationships for precipitation were developed because the instrumental data indicate that rain and snow are more heterogeneous in the region than temperature. For each temperature variable, two lapse rates were determined for the San Bernardino Mountains, two for the Cuyamaca and Laguna Mountains, and one each for the San Jacinto Mountains and Mount Palomar. For precipitation, six equations were determined for the San Bernardino Mountains, three for the Cuyamaca and Laguna Mountains, and one each for the San Jacinto Mountains and Mount Palomar. The number of lapse rates/equations for each mountain group reflects the availability of the data, the geographic extent of the ranges and surface

samples, and the topographic complexity of the ranges. All relationships are for the cismontane side (west of the eastern, desert crest) of the coastal mountains. The individual lapse rates and equations are listed in Table 2, along with their assignments to the surface samples.

For temperature, the lapse rates use foothill and montane endpoints. The rates were calculated as the linear change in temperature for change in elevation. For the one near-coastal sample (41), the temperatures of a specific reporting station were used.

For precipitation, three types of calculation were used: a) where only foothill and montane endpoints are available, linear equations were employed; b) in two cases in the San Bernardino Mountains, weighted averages of two linear equations were calculated (the weighting scheme is described in Appendix 1); and c) where the data allow, equations were fitted using information from a foothill station, an intermediate station, and a montane station or high-elevation map location. In these latter cases, four functional types were examined as estimating equations for the precipitation-elevation relationship: linear, exponential, logarithmic, and power functions. With two exceptions, the best fitting of these equations were used. In the first exception, two of the functions fit similarly well and the equation chosen was to be used to extrapolate to elevations well beyond the range of the data points; the second best, linear, fit was chosen since the better fit rose sharply outside of the range of the data. In the second exception, three of the functions fit almost identically well; the second best, linear, equation was chosen as the simpler functional form. Due to its restricted period of record, Mill Creek was used as an intermediate station only when: a) it provided a functional relationship significantly different from that determined by the corresponding foothill and montane endpoints; and b) the average precipitation values for the corresponding endpoints during the Mill Creek period of record were very close to their values during the normative period of record. For the one near-coastal sample, the precipitation value was taken from the *California Annual Precipitation* map (1999).

The temperature lapse rates are based solely on instrumental data. Four of the precipitation equations use precipitation values interpolated from the *California Annual Precipitation* map (1999) to give high-elevation endpoints where no instrumental data are available. The map isohyets were cross-checked against the instrumental data at the Lake Arrowhead, Big Bear Lake, and Cuyamaca station sites.

Validation of the Modern Pollen Surface Sample Set for Use in the MAT Procedure

The basic method of validation used here follows that of Prell (1985), Bartlein and Whitlock (1993), and Davis et al. (2000). In this approach, the mod-ern climate values assigned to the surface sample sites are reconstructed using the same technique that is employed for paleoclimate reconstruction, by selecting analogs for each sample from among the *other* surface samples (the sample whose site conditions are being reconstructed is not allowed to serve as an analog for itself). A weighted average of the climate values associated with the analogs for a particular sample gives the reconstructed climate for the sample; the weights are proportionate to the inverses of the squared chord distances (SCD's) between the pollen assemblages of the target sample and its analogs. The reconstructed climate for each site is then compared to its assigned value. (Mathematically, use of the inverse SCD for weighting determines that the same-sample data must be excluded from the reconstruction procedure, since the inverse of a sample's SCD with itself is 1/0, which is undefined.) Definition of the SCD is given in Wahl (2003), where some of its characteristics and issues concerning its use in the MAT are described. Extended consideration of the SCD and its characteristics for use in the MAT is given in Overpeck et al. (1985), Gavin et al. (2003), and Wahl (in press). The pollen taxa included in the SCD calculations are the same as those used in the companion paper to examine patterns of SCD relationships among the elements of the surface sample set (cf. Fig. 4 in Wahl 2003).) The same procedure was also used to test elevation reconstructions, since reconstruction of the "apparent" elevation of study sites at different times in the past (in terms of the vegetation growing at a site in relation to its modern vegetation) is an important Quaternary paleoecological tool used in montane portions of western North America (e.g., Anderson et al. 2000).

This basic method was extended by reconstructing each of the climate variables and elevation using five different SCD cutoff values for analog selection, 0.15, 0.20, 0.25, 0.30, and 0.35 (a given cutoff value defines the SCD below which two pollen assemblages are considered similar enough to be analogous). Employing a range of SCD cutoffs allows the quality of the reconstructions to be used as a gauge for determining which cutoff level(s) recover maximal climate and elevation information. The range of cutoff values chosen brackets the range of best-performing values determined for this surface sample set in terms of separating like from unlike vegetation (Wahl 2003; Wahl in press). Two thresholds for the minimum number of analogs required to reconstruct were also examined, in order to evaluate the extent to which restricting reconstructions to three or more analogs might eliminate relevant information. The combination of five cutoff values with two levels for the minimum number of analogs gives ten reconstruction scenarios for each of the four climate variables and elevation in a 3-way factorial design.

Samples 21 and 35 (Table 3) were not included

TABLE 2. CLIMATE ASSIGNMENT FORMULAS AND SINGLE-POINT DATA USED TO DETERMINE SURFACE SAMPLE CLIMATE VALUES. *January and July temperature formulas* are rates of change calculated from station values as end-points. The **bold** values are the lapse rates in °C/km elevation. The italicized value before the lapse rate is the low station's temperature; the italicized value subtracted from "Elevation" is the low station's elevation. *Precipitation formulas* are fitted linear, logarithmic, or exponential equations as indicated. The slope values for the linear equations are lapse rates in cm/km elevation, and are highlighted in **bold.** Four high-elevation endpoint values were taken from the *California Annual Precipitation* map (1999), as indicated. *Notes* (1) Mill Creek not used as intermediate station. Fit between endpoints nearly identical to fit with Mill Creek included; explained in text. (2) r^2 for linear form = 0.987. Linear form used instead of exponential fit with r^2 of 0.997; explained in text. (3) Equation fitted with elevation in m; factor 6.90775 (ln 1000) corrects for conversion of m to km. r^2 = 0.945. (4) r^2 = 0.967. (5) r^2 = 0.971. (6) r^2 for linear form = 0.992. Linear form used instead of power function fit with r^2 of 0.999; explained in text.

End- & mid-point stations (names of stations/map sites)	Formula for calculation (°C temp.) (cm precip.)		Associated surface samples (#'s follow Wahl 2003)
	"Elevation" in formulas indicates surface sample elevation in km		
January temp. (monthly mean)			
Redlands-Big Bear Lake	*11.61 + (−***6.576****(Elevation − 0.4017))*		1, 2, 3, 4, 5, 6, 10, 12, 13, 15, 16, 23
Redlands-Lake Arrowhead	*11.61 + (−***7.355****(Elevation − 0.4017))*		7, 8, 9
Idyllwild Fire Dept-Mount San Jacinto WSP	*4.75 + (−***5.062****(Elevation − 1.6398))*		11, 14, 18, 19, 20
Alpine-Cuyamaca	*12.02 + (−***8.369****(Elevation − 0.5288))*		17, 21, 22, 24, 25, 26, 27, 28, 31, 32, 33, 34, 35, 37, 38, 39, 40
Alpine-Julian Wynola	*12.02 + (−***7.336****(Elevation − 0.5288))*		29
Escondido (1 & 2)-Palomar Mountain Observatory	*12.06 + (−***4.028****(Elevation − 0.2009))*		30, 36
La Mesa Station value	13.65		41
July temp. (monthly mean)			
Redlands-Big Bear Lake	*25.79 + (−***4.983****(Elevation − 0.4017))*		1, 2, 3, 4, 5, 6, 10, 12, 13, 15, 16, 23
Redlands-Lake Arrowhead	*25.79 + (−***4.472****(Elevation − 0.4017))*		7, 8, 9
Idyllwild Fire Dept-Mount San Jacinto WSP	*20.38 + (−***4.737****(Elevation − 1.6398))*		11, 14, 18, 19, 20
Alpine-Cuyamaca	*24.30 + (−***3.614****(Elevation − 0.5288))*		17, 21, 22, 24, 25, 26, 27, 28, 31, 32, 33, 34, 35, 37, 38, 39, 40
Alpine-Julian Wynola	*24.30 + (−***2.762****(Elevation − 0.5288))*		29
Escondido (1 & 2)-Palomar Mountain Observatory	*23.25 + (−***0.384****(Elevation − 0.2009))*		30, 36
La Mesa Station value	22.49		41
Annual precipitation			
Redlands (instrumental)-San Bernardino Mt. (map)	(**28.7***Elevation) + 21.051	**(1)**	5, 6, 15, 16, 23
Redlands-Mill Creek-Lake Arrowhead	(**60.8***Elevation) + 2.5678	**(2)**	*Not Applicable*: calculated for use with following two rates
70% Redlands-San Bernardino Mt. + 30% Redlands-Mill Creek-Lake Arrowhead	0.7*((**28.7***Elevation) + 21.051) + 0.3*((**60.8***Elevation) + 2.5678)		8, 9, 12
50% Redlands-Mill Creek-Lake Arrowhead + 50% Redlands-San Bernardino Mt.	0.5*((**28.7***Elevation) + 21.051) + 0.5*((**60.8***Elevation) + 2.5678)		7
Redlands-Mill Creek-Big Bear Lake	19.666*((LN Elevation) + 6.90775) − 85.835	**(3)**	13
Big Bear Lake (instrumental)-Onyx Peak (map)	(**49.9***Elevation) − 45.329		1, 2, 3, 4, 10
Idyllwild Fire Dept (instrumental)-Mount San Jacinto (map)	(**24.3***Elevation) + 26.733		11, 14, 18, 19, 20
Alpine-Descanso Ranger Stn-Cuyamaca	27.24* EXP (0.8*Elevation)	**(4)**	17, 24, 26, 27, 28, 31, 32, 33, 38, 40

Table 2.   Continued.

End- & mid-point stations (names of stations/map sites)	Formula for calculation (°C temp.) (cm precip.)		Associated surface samples (#'s follow Wahl 2003)
Alpine-Descanso Ranger Stn-Julian Wynola	29.75*EXP (0.7*Elevation)	**(5)**	29
Alpine-Descanso Ranger Stn (instrumental)-Mt. Laguna (map)	(**25.5***Elevation) + 30.159	**(6)**	21, 22, 25, 34, 35, 37, 39
Escondido (1 & 2)-Palomar Mountain Observatory	(**22.1***Elevation) + 33.330		30, 36
Interpolated map data	27.94		41

in the reconstruction analysis because their pollen representation characteristics cause them to have only spurious analogies with other vegetation types (Wahl 2003). Pollen representation refinements to the analog method (Calcote 1998; Wahl 2003) were not employed to restrict analog selection, so that the pure impact of varying the SCD cutoff level could be assessed. Possible enhancements using this technique are described in the "Discussion" section.

Results

Climate Assignments

The climate values assigned to the surface sample sites are listed in Table 3. Four climate variables were assigned: January average daily mean temperature, July average daily mean temperature, the average of January and July temperature, and annual precipitation. Average January and July temperature is included as an approximation of annual temperature, at the scale of resolution available in some paleoclimate model experiments that have been extensively compared to paleoclimate data (COHMAP members 1988; Thompson et al. 1993). (These experiments simulate climate as "snapshots" of January or July conditions.) The numbering of the samples conforms to the numbering in Wahl (2003, Table 1), where site information for the samples is also given. Figure 1 shows the range of values for each of the assigned variables in graphical form, categorized by the major elevation-related vegetation groups from which the samples were taken; the vegetation groups are described in Wahl (2003). Figure 2 shows the mean and range of variation for each variable for each of the vegetation groups.

The January temperature lapse rates are close to typical measured adiabatic rates of −6–7°C km⁻¹ for dry air (which exhibit significant localized variation, Wallace and Hobbs 1977). The July temperature lapse rates are closer to the typical humid air adiabatic lapse rate of ~ −4°C km⁻¹ (Wallace and Hobbs 1977), likely reflecting the greater humidity characteristic of the cismontane region in the late spring and summer. The values for the Escondido (1&2)/Palomar Mountain Observatory temperature lapse rates are unusually low in terms of their ab-

solute value, especially for July, a characteristic noted for other near-coastal large mountains in the region. For example, the lapse rates determined here for Escondido/Mt. Palomar (including precipitation) are highly similar to those observed for the Pasadena (263 m)/Mt. Wilson (1740 m) transect in Los Angeles County (Major 1988, p. 50). Both mountains form imposing scarps of similar elevation only ~50 km from the Pacific Ocean. The summer lapse rates for these mountains may be particularly influenced by the temperature inversion associated with late spring/summer coastal fogs, which typically occurs at elevations including the Mt. Palomar and Mt. Wilson observing stations (University Corporation for Atmospheric Research, Cooperative Program for Operational Meteorology, Education, and Training, "West Coast Fog" module *http://meted.ucar.edu*). In comparison, other regional paleoecological studies that have developed quantitative temperature estimates using lapse rates (Adam and West 1983 in coastal northern California; Anderson et al. 2000 in the interior Southwest) have used values in the typical range for dry adiabatic processes.

Validation

Table 4 and Figures 3 and 4 give the results of the validation tests. Table 4 gives regression results for comparisons of the reconstructed and assigned values. The regressions marked with an asterisk indicate the cutoff scenario(s) with the best reconstructions, as determined by a combination of slope closest to one and intercept closest to zero (together representing the most unbiased, or accurate, estimates) and highest r² (representing the most precise estimates). In cases of tradeoffs between slightly higher r² and slope slightly further away from one (e.g., January temperature for the 0.25 and 0.30 cutoffs), greater importance was assigned to the slope parameter; i.e., small degradations in precision are considered appropriate to sacrifice for lowering bias to near zero. Figure 3 shows example scatter plots and fitted regression lines for one of the best-case scenarios noted in Table 4 (January temperature).

Comparison of the slope, intercept, and r² values across scenarios by use of standard techniques for

TABLE 3. SURFACE SAMPLE SITE ELEVATION AND CLIMATE CHARACTERISTICS. Numbering and vegetation names follow Wahl (2003).

Sample	Main vegetation category	Vegetation name	Elevation (m)	January	July	Jan/July average	Annual Precip. (cm)
1	**Upper- & mid-Montane Conifer-dominated Forests (1–20)**	Lodgepole/Jeffrey/Fir Forest	2774	-3.99	13.97	4.99	93.09
2		Western Juniper/Lodgepole Forest/Woodland	2746	-3.81	14.11	5.15	91.70
3		Fir/Lodgepole Forest	2707	-3.55	14.30	5.38	89.75
4		Fir/Limber/Juniper Woodland	2597	-2.83	14.85	6.01	84.26
5		Fir/Jeffrey/Lodgepole Forest	2499	-2.18	15.34	6.58	92.77
6		Jeffrey/Fir Forest	2481	-2.06	15.43	6.68	92.26
7		Pine/Fir/Oak Forest	2243	-1.93	17.56	7.81	112.18
8		Pine/Fir Forest	2228	-1.82	17.62	7.90	100.91
9		Pine/Fir Forest	2228	-1.82	17.62	7.90	100.91
10		Pine/Western Juniper/Fir Forest	2438	-1.78	15.64	6.93	76.33
11		Lodgepole/Limber Forest	2926	-1.76	14.29	6.26	97.83
12		Pine/Fir Forest	2402	-1.54	15.82	7.14	107.57
13		Pine/Fir Forest	2286	-0.78	16.40	7.81	66.27
14		Lodgepole/Fir Forest	2682	-0.53	15.44	7.46	91.91
15		Fir/Pine Forest–Aspen Grove (> dense with Aspen)	2170	-0.02	16.98	8.48	83.33
16		Fir/Pine Forest–Aspen Grove (< dense with Aspen)	2170	-0.02	16.98	8.48	83.33
17		Pine/Fir/Oak/Cedar Forest	1890	0.63	19.38	10.00	123.56
18		Pine/Alder/Fir Forest	2405	0.88	16.76	8.82	85.17
19		Pine/Fir Forest	2405	0.88	16.76	8.82	85.17
20		Pine/Fir Forest	2402	0.89	16.77	8.83	85.10
21	**Lower-Montane Conifer-Oak Forests, Meadows, Chaparral (21–33)**	Manzanita Chaparral	1692	2.29	20.10	11.19	73.31
22		Pine/Oak Forest	1829	1.14	19.60	10.37	76.80
23		Oak/Conifer Forest	1682	3.19	19.41	11.30	69.32
24		Cedar/Pine/Oak/Fir Forest	1573	3.28	20.53	11.90	95.88
25		Pine/Oak Forest	1554	3.44	20.59	12.02	69.79
26		Oak/Cedar/Pine Forest	1451	4.30	20.97	12.63	86.96
27		Oak/Cedar Stand-in Pine/Oak/Cedar/Fir Forest	1448	4.33	20.98	12.65	86.75
28		Pine/Oak Open Forest Clearing	1439	4.40	21.01	12.71	86.13
29		Oak/Pine Forest	1228	6.89	22.37	14.63	70.28
30		Cedar/Oak/Fir Forest-Burn Site	1573	6.53	22.72	14.63	68.09
31		Meadow–in Pine/Oak/Cedar/Fir Forest	1439	4.40	21.01	12.71	86.13
32		Meadow–in Pine/Oak/Cedar/Fir Forest	1434	4.44	21.03	12.74	85.79
33		Mixed Chaparral–Mt. Mahogany dominated	1384	4.86	21.21	13.04	82.42
34	**Steppe, Mixed Chaparral, Oak Woodland (34–39)**	Sagebrush Steppe (> open phase)	1132	6.97	22.12	14.55	59.03
35		Sagebrush Steppe (> closed phase)	1125	7.03	22.15	14.59	58.85
36		Oak Woodland (> closed phase)	1414	7.17	22.78	14.98	64.58
37		Oak Woodland (> open phase)	1073	7.47	22.33	14.90	57.52
38		Mixed Chaparral	1091	7.31	22.27	14.79	65.20
39		Mixed Chaparral	1061	7.57	22.38	14.97	57.21
40	**Chamise Chaparral, Sage scrub**	Chamise Chaparral	817	9.61	23.26	16.43	52.37
41		Coastal Sage Scrub	244	13.65	22.49	18.07	27.94
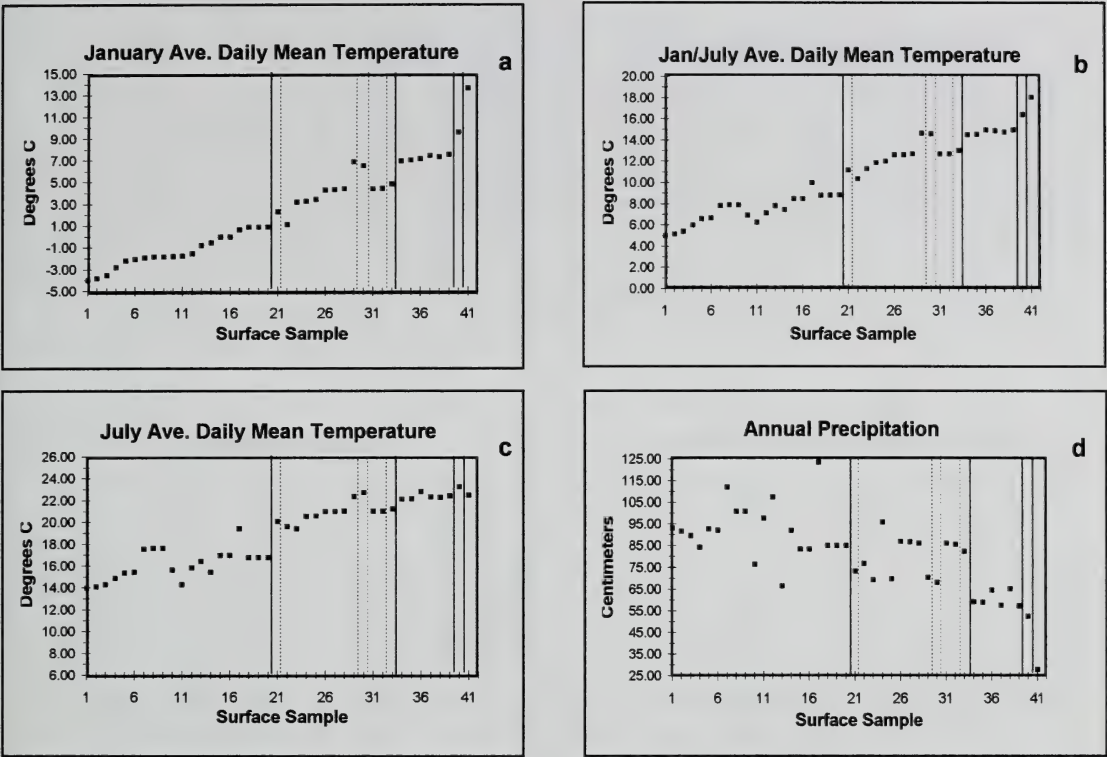
FIG. 1. Temperature and precipitation values for surface samples. Sample numbers conform to Table 3. From left to right, categories set off by heavy dark lines are: 1) Upper- and Mid-Montane Conifer-dominated Forests; 2) Lower-Montane Vegetation; 3) Steppe, Mixed Chaparral, and Oak Woodland; 4) Chamise Chaparral; and 5) Coastal Sage Scrub. Vegetation types within the Lower-Montane category are set off by dashed lines; from left to right these are: manzanita chaparral, conifer-oak forests, a forest burn site, lower-montane meadows, and higher-elevation mixed chaparral.

testing differences between computed parameters is not appropriate since each regression gives the results of the reconstruction procedure for a different population of potential reconstructions (R. D. Cook personal communication). (Different cutoff levels determine different numbers of selected analogs and different absolute weights for each set of chosen analogs.) However, since each parameter reported is an estimate of the expected value of the distribution of that parameter, it is reasonable to evaluate these expected values one against another in a qualitative manner (R. D. Cook personal communication). While these comparisons cannot be subjected to strict confidence interval testing at specified levels of risk, it is more reasonable to accept the reported parameters closest to the defined optima as likely to identify the best reconstruction scenarios than it is to reject comparison entirely and assume that the reported parameters carry no comparative information.

Figure 4 shows the numerical anomalies (reconstructed value minus assigned value) for the individual surface samples, organized by vegetation type. The anomalies for precipitation and elevation are given as percentages, in order to express them in terms of relative measure. The anomaly values for temperature are given in degrees, since relative temperature differences are represented by degree differences, regardless of plus/minus magnitude. The reconstructions in each figure are based on two or more analogs being chosen by a sample. Figure 4a shows anomalies for reconstructions at a SCD cutoff level of 0.20 and Figure 4b shows anomalies at a cutoff of 0.25. These combinations of reconstruction parameters yield the best accuracy and precision for temperature and elevation reconstructions, as discussed below, and also yield the lowest mean anomaly values for these variables. The mean anomalies for precipitation reconstruction also are lowest at the 0.20 cutoff level, although less bias and somewhat greater precision in terms of regression analysis of the reconstructions is obtained at higher cutoffs.

Results are not reported or discussed separately for the average of January/July temperature to avoid redundancy, since the reconstruction performance for this variable is highly similar to that of the other two temperature variables.
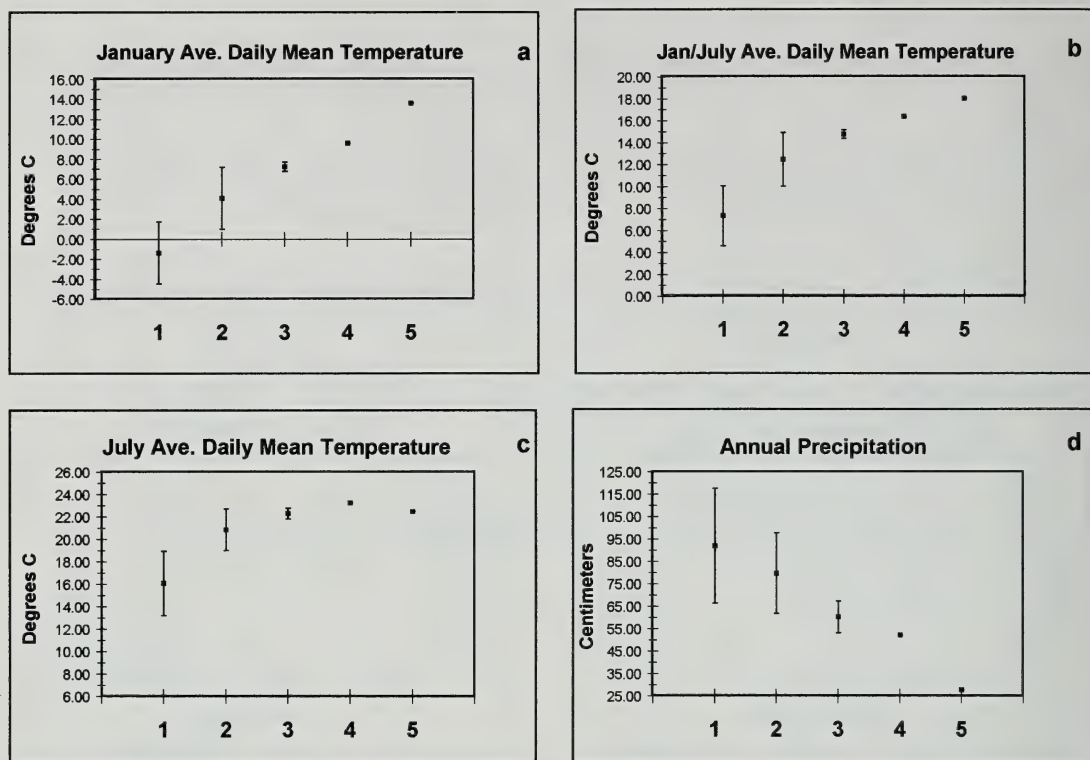
FIG. 2. Climate ranges of vegetation categories. Categories conform to Table 3 and Figure 1: 1) Upper- and Mid-Montane Conifer-dominated Forests; 2) Lower-Montane Vegetation; 3) Steppe, Mixed Chaparral, and Oak Woodland; 4) Chamise Chaparral; and 5) Coastal Sage Scrub. Data points and error bars for 1–3 show the mean and 2× standard deviation for all samples in the category. Data points for 4–5 show the value for the one sample in the category.

DISCUSSION

Characteristics of Assigned Climate Values and Relation to Vegetation

The most salient characteristic of the climate values is the difference between the variances of the temperature and precipitation values within and among vegetation categories. This characteristic is evident in the greater relative spread of the precipitation values in Figure 1, and more analytically in the overlap and width of the 2× standard deviation ranges in Figure 2. Figures 1 and 2 highlight the reduced climatic separation between the mid- and upper-montane conifer-dominated forests and the lower-montane vegetation types of cismontane southern California in terms of precipitation relative to temperature. These data suggest that temperature, rather than precipitation, is the primary climate factor responsible for the dominance of pine-fir forests in the mid- and upper-montane portions of the region—with the complete exclusion of oaks (arboreal and shrub) and lower-montane chaparral at higher elevations. Neilson and Wullstein (1983) relate winter cold and spring freezes to the close association of the northern range limit of *Quercus gambelii* with the " 'polar front' gradient"

in northern Utah. The higher elevations of the southern California mountains would be more likely than lower-montane areas to experience temperatures cold enough to damage adult stems unprotected by snow cover and to develop severe frost after conditions warm enough to initiate break from dormancy, analogous to the latitudinal distribution of similar limiting conditions in the northern Great Basin (Neilson and Wullstein 1983).

Overall, January average daily mean temperature is most closely associated with differences in the vegetation of the surface samples (Fig. 2), consistent with the interpretation that winter cold could partially explain the dominance of conifer species in the mid-and upper-montane forests and woodlands. This variable has the least overlap among samples of the five major vegetation categories. In particular, the lower-montane and steppe/mixed chaparral/oak woodland vegetation categories are well distinguished from each other and from the chamise chaparral and coastal sage scrub samples. July temperature separates the lower-montane and steppe/mixed chaparral/oak woodland categories slightly less well than January temperature, and does not separate the lower-montane and steppe/

TABLE 4. VALIDATION RESULTS: REGRESSIONS COMPARING ASSIGNED AND RECONSTRUCTED CLIMATE AND ELEVATION.[a, b]
[a] The best regressions for each climate parameter and elevation (defined as combinations of slope nearest one, intercept nearest zero, and highest r^2—with close tradeoffs between these characteristics decided in favor of the slope parameter) are marked with asterisks. [b] In these regressions, reconstructed values and assigned values are "placed" on the "x" and "y" axes, respectively. This placement follows Bartlein, Webb, and Fleri (1984) and Cook and Weisberg (1999) for comparison of actual values of a variable with estimates of the same variable. (The convention in regression is to place a variable of interest on the "y" axis whose relationship to the conditional distribution of another variable, placed on the "x" axis, is being considered. In "actual vs. estimated" comparisons, the interest is in understanding how the actual [here "assigned"] values—which are not knowable in the real prediction/reconstruction period—are related to the conditional distribution of the estimated [here "reconstructed"] values—which *are* known in the prediction/reconstruction period [Cook and Weisberg 1999].)

Reconstructed parameter	SCD cutoff	Min. # analogs	Slope	Intercept	r^2	n
January temperature (average monthly mean °C)						
	0.15	2	0.8781	0.1222	0.6517	27
	0.15	3	0.8566	0.0925	0.5427	24
	0.20	2	0.9182	0.1993	0.7098	32
	0.20	3	0.9317	0.1308	0.6717	28
	0.25	2	*0.9988	*0.3071	*0.7266	35
	0.25	3	*1.0060	*0.3191	*0.7140	33
	0.30	2 & 3	1.0586	0.2883	0.7545	36
	0.35	2 & 3	1.0570	0.3273	0.7382	36
July temperature (average monthly mean °C)						
	0.15	2	0.9614	0.6014	0.6859	27
	0.15	3	0.9590	0.6425	0.5848	24
	0.20	2	*0.9782	*0.4589	*0.7305	32
	0.20	3	*1.0066	*0.0869	*0.6919	28
	0.25	2	*1.0147	*0.0576	*0.7125	35
	0.25	3	*1.0236	*0.2016	*0.6959	33
	0.30	2 & 3	1.0637	0.9302	0.7306	36
	0.35	2 & 3	1.0670	0.9633	0.7187	36
Precipitation (annual cm)						
all data	0.15	2	0.5333	39.882	0.1447	27
all data	0.15	3	0.6043	33.850	0.1403	24
lowest/highest outliers omitted	0.15	3	0.7077	24.926	0.2562	22
all data	0.20	2	0.6481	30.517	0.1458	32
all data	0.20	3	0.6673	29.323	0.1565	28
lowest/highest outliers omitted	0.20	3	0.7241	24.164	0.2503	26
all data	0.25	2	0.7659	19.942	0.1688	35
all data	0.25	3	0.7658	19.939	0.1687	33
lowest/highest outliers omitted	0.25	3	0.8774	10.105	0.2812	31
all data	0.30	2 & 3	0.8169	15.085	0.1846	36
lowest/highest outliers omitted	0.30	2 & 3	0.9240	5.6360	0.2975	34
all data	0.35	2 & 3	*0.8418	*12.870	*0.1946	36
lowest/highest outliers omitted	0.35	2 & 3	*0.9535	*3.0361	*0.3139	34
Elevation (meters above sea level)						
	0.15	2	0.9992	18.123	0.7165	27
	0.15	3	0.9487	141.52	0.6216	24
	0.20	2	*0.9985	*7.4306	*0.7647	32
	0.20	3	*1.0309	*68.226	*0.7303	28
	0.25	2	1.0438	129.91	0.7523	35
	0.25	3	1.0562	159.69	0.7375	33
	0.30	2 & 3	1.0796	199.14	0.7648	36
	0.35	2 & 3	1.0858	218.99	0.7490	36
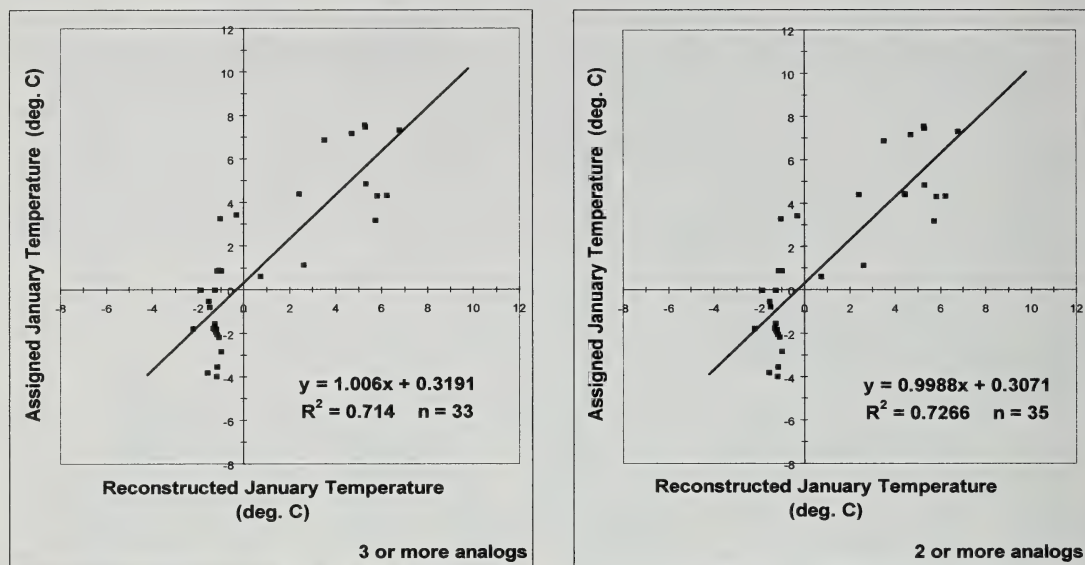
Fig. 3.   Validation results: scatter diagrams and regressions comparing assigned and reconstructed January temperature at 0.25 squared chord distance (SCD) cutoff level. Results for July temperature and elevation reconstructions are highly similar.

mixed chaparral/oak woodland categories well from the coastal sage scrub sample. The reversal in July temperature between the chamise chaparral and coastal sage scrub samples goes against the general elevation-temperature relationship in the region, but is an expectable result of the cool, near-coastal fogs that are characteristic in the late spring and summer (*Climates of the States* 1985).

The precipitation value for sample 17 on Mt. Cuyamaca in San Diego County (123.6 cm/yr; Table 3, Fig. 1) is the largest of all the samples, and is unusual for its elevation. The value determined here is consistent with precipitation reported for the higher parts of the Cuyamaca Mountains in the published flora of San Diego County (Beauchamp 1986). It is also worth noting that the Cuyamaca Mountains receive the highest average summer rainfall in the southern California region (Hamilton 1983). The high precipitation at this site has been recognized since pre-historic times; the name Cuyamaca is a Latinization of the Native Californian name for the area, meaning "the place where it rains" (Cuyamaca Rancho State Park Museum, California Department of Parks and Recreation).

Characteristics of MAT Validation of the Modern Pollen Surface Sample Set

Best MAT Cutoff Values and General Character-istics of Climate and Elevation Reconstructions. For January temperature, the best analog-based re-constructions occur at the SCD cutoff level of 0.25 (Table 4). For July temperature, cutoffs of 0.20 and 0.25 both yield the best reconstructions. Elevation is best reconstructed at a cutoff level of 0.20. Over-all, the reconstructions for the temperature variables and elevation are very similar in their characteris-tics. All exhibit nearly zero bias and similarly good precision ($r^2 = 0.69$–0.76) at their best cutoff val-ues, and give good quality reconstructions for the overall range of cutoffs bounded by 0.20 and 0.35. These variables are also generally characterized by more rapid improvement in reconstruction quality between cutoffs of 0.15 and 0.20 in relation to the decline in quality from the best cutoff(s) to 0.35 (especially in terms of precision for July tempera-ture and elevation).

The range of best cutoff values for temperature and elevation is nearly identical to that determined independently for the surface sample set in terms of discriminating between samples from like and unlike vegetation (Wahl in press). This congruence of results suggests that the pollen assemblages of the surface samples have similar information ca-pacities in terms of the temperature/elevation and vegetation characteristics of the samples. The rel-atively rapid decline in reconstruction quality at SCD's below the best range and the relatively slow decline above it also parallel the sharp increase in false negatives below the best range and the slow increase in false positives above it in terms of veg-etation discrimination (Wahl in press). This char-acteristic indicates that conservative cutoff levels set below the best range would eliminate important temperature/elevation information, relatively quick-ly leading to increased imprecision and bias, where-as cutoffs set somewhat above the best range would degrade performance less critically. All of these variables exhibit improved precision when the min-

a

b
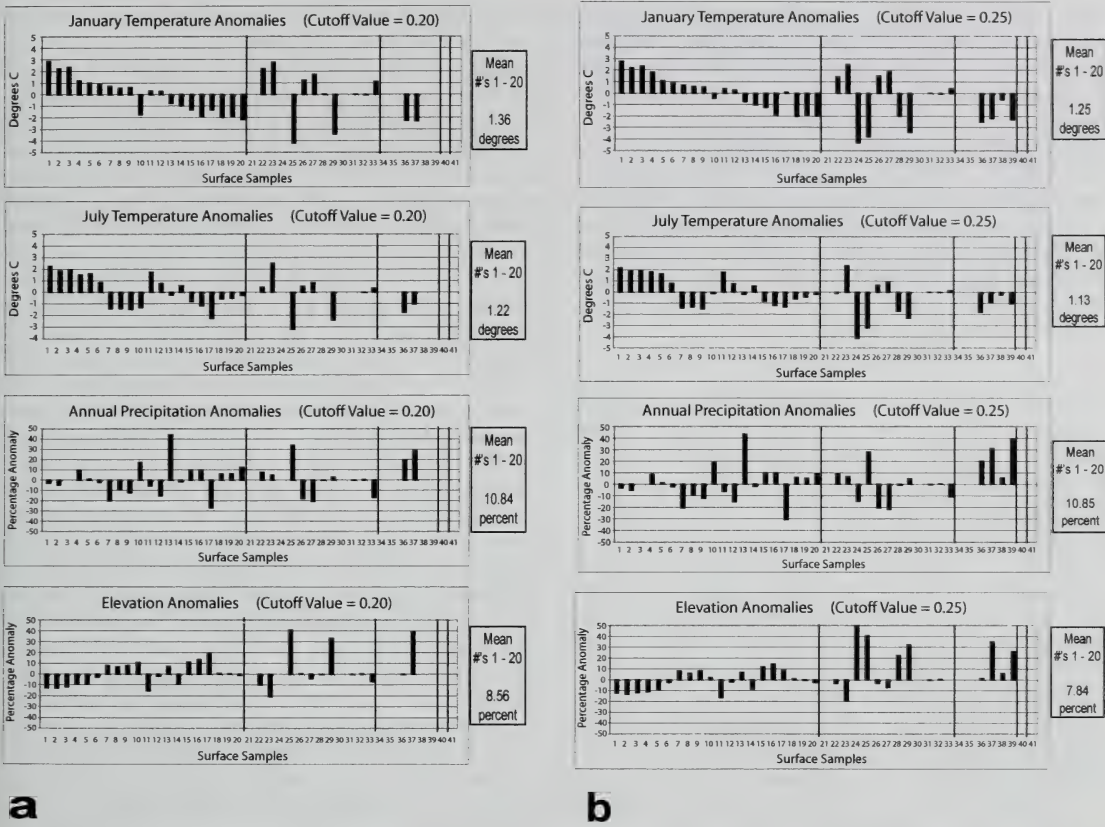
FIG. 4. Reconstruction anomalies (reconstructed value minus assigned value) for the individual surface samples, organized by vegetation type. (a) Anomalies at a squared chord distance (SCD) cutoff value of 0.20; (b) anomalies at a SCD cutoff value of 0.25. Reconstructions are based on 2 or more analogs; samples without anomalies were not reconstructed because they had too few analogs. The mean values reported average the absolute values of the anomalies, so that positive and negative values do not cancel each other.

Vegetation categories set off by vertical lines are, from left to right: a) Upper-and Mid-Montane Conifer-dominated Forests (1–20); b) Lower-Montane Vegetation (21–33); c) Steppe, Mixed Chararral, and Oak Woodland (34–39); d) Chamise Chaparral (40); and e) Coastal Sage Scrub (41). Sample numbering and categories conform to Table 3 and Figure 1.

imum number of analogs allowed in reconstruction is set at two instead of three (at the cutoff values for which this comparison is relevant, 0.15–0.25) indicating that important information is also being discarded at the higher minimum requirement.

The most significant limitation for the reconstruction of temperature and elevation is that the reconstructed values at lower temperatures/higher elevations do not reflect the full range of the assigned values. In Figure 3 this phenomenon is shown for January temperature by the relatively large vertical spread of points for a less-wide horizontal spread at lower temperature. The scatter plots for July temperature and elevation look much like those for January temperature. The means of the reconstructed and assigned values in these ranges are nearly identical, however, which contributes to the overall lack of bias in the reconstructions. Based on these validations, paleo-temperature and

apparent elevation reconstructions developed with this surface sample set can be expected to be generally unbiased and relatively precise, although the range of lower-temperature/higher-elevation reconstructions can be expected to be slightly compressed in comparison to the true variation of these variables in paleo-history in the study region.

For annual precipitation, the best reconstructions in terms of regression analysis parameters occur at the SCD cutoff level of 0.35, with reasonably low levels of bias but relatively poor precision (Table 4). Even with the highest and lowest outliers eliminated from the regressions, the highest r^2 obtained by any precipitation reconstruction scenario is only 0.31. This reduced precision is expectable from the relatively high degree of variation in precipitation both within and between the mid- and upper-montane conifer-dominated forests and the lower-montane vegetation types in the

study region (Figs. 1, 2). In addition, the pattern of increased precision associated with lowering the minimum number of analogs exhibited by the temperature and elevation variables is not apparent for the precipitation reconstructions, at the cutoff values for which this comparison is relevant (0.15–0.25). Because of these characteristics, quantitative reconstructions of paleo-precipitation derived from this surface sample set generally can be expected to be somewhat less precise than those for temperature and elevation. The lowest mean absolute anomaly for precipitation reconstruction occurs at a cutoff of 0.20.

Reconstruction characteristics of vegetation groups and particular samples. The most salient feature of the individual anomalies (Fig. 4) is that most of reconstructions at the best SCD cutoffs (0.20 and 0.25) are within ±2°C for the temperature variables and ±15% for elevation. Precipitation has a greater proportion of large (>±20%) anomalies, as expected, but also has numerous quite small anomalies at these cutoffs, which make its average anomaly relatively small. A second important characteristic is the overall excellent performance of the reconstructions for all the variables (including precipitation) within the conifer-dominated forest category (samples 1–20), even bearing in mind that possible restrictions of analogs with conifer-oak forests (Wahl 2003) were not done in this analysis. Only the precipitation reconstructions for samples 13 and 17 deviate greatly from this pattern. This characteristic is of particular significance for paleo-reconstruction, since the predominant selection of analogs by the fossil record for which the surface samples were developed as a calibration set is from the conifer forest group (Wahl 2002; E. Wahl, Holocene paleoenvironmental reconstruction in the southern California Peninsular and Transverse Ranges, *in preparation*). The lowest mean absolute anomalies for the conifer-dominated forest category are shown in Figure 4: 1.25° for January temperature, 1.13° for July temperature, 7.84% for elevation (all at a SCD cutoff of 0.25), and 10.84% for annual precipitation (at a cutoff of 0.20).

Seven samples (13, 17, 24, 25, 29, 37, and 39) have particularly large anomalies in one or more of the reconstructed variables. Within the conifer forest category, sample 13 has erroneously high reconstructed precipitation because it is the site with the lowest assigned precipitation in this group, reflecting a precipitation shadow in the local Big Bear Valley area (Table 3, Fig. 1). The vegetation and pollen representation at this site are typical of the conifer-dominated forests, causing it to select analogs that have significantly higher precipitation. Sample 17 is nearly the opposite case, having the highest precipitation in the entire surface sample set (Table 3, Fig. 1). It necessarily selects analogs with less moisture, causing its reconstructed values to be erroneously low. This is an intractable problem for

end-members of a calibration set in this kind of verification test of the MAT.

The greatest inaccuracies are generally associated with three of the conifer-oak forest samples in the lower-montane vegetation category (24, 25, 29). Samples 24 and 25 have relatively high conifer/*Quercus* pollen ratios (Wahl 2003), which cause them to select most of their analogs from the higher, cooler conifer forest category. Since the conifer-oak forests of the region can be reliably distinguished from the conifer-dominated forests on the basis of their *Quercus* pollen representation (Wahl 2003), a potential way to eliminate some of the reconstruction inaccuracy for these samples would be to constrain the set of analogs they are allowed to select—to samples with *Quercus* pollen proportions greater than the maximum *Quercus* proportion among the conifer-dominated forests. Sample 29 reconstructs temperature and elevation poorly because it is the lowest-elevation representative of its group, being essentially in the transition between the lower-montane and steppe/mixed chaparral/oak woodland vegetation categories (Table 3; Wahl 2002). The analogs it selects are mostly higher, cooler conifer-oak forests, with only one analog from the conifer-dominated forests. Because of this pattern of analog selection, the bias in its reconstruction cannot readily be corrected using the constrained-selection approach suggested for samples 24 and 25.

Samples 37 (oak woodland) and 39 (mixed chaparral) have precipitation and elevation reconstructions biased to higher values because they select some of their analogs from higher, wetter sites in the lower-montane vegetation category. A constrained-selection approach might also be employed with these samples for analogies with conifer-oak forest sites, since the latter generally have much higher representation of *Pinus* pollen than the oak woodland and chaparral samples (Wahl 2003).

Summary Considerations and Implications for Paleoenvironmental Reconstruction

The ability of the assigned values to reflect highly local variations of the regional climate—in particular the high precipitation value for Mt. Cuyamaca (sample 17) and the precipitation shadow in the Big Bear Valley area (sample 13)—indicates that the assignment methods are well-calibrated to the region's fine-scale climate patterns. Although the results of the validation procedure show that unbiased and relatively precise paleoclimate reconstructions can be anticipated from use of the new modern pollen data set, especially for the temperature variables, the high precipitation reconstruction errors for sites 13 and 17 (which cannot be reduced by constraining analog selection among vegetation categories) suggest that the information capacity of the MAT using these pollen data is not as fine-grained spatially as that of the underlying climate data. While it would be optimal to have

additional fine-grained information capacity in the pollen/MAT tool, it is better that information "further down" in the analytical structure (the climate assignments) has the higher information capacity, as opposed to the reverse. This is true in general for any calibration system—the information content of the system, and thereby its ability to act as an analytical or reconstruction tool, is fundamentally constrained by the signal-to-noise ratio ("noise floor") of its most basic elements. In this case, the pollen-climate relationship developed via the MAT appears to be slightly more limiting to the potential accuracy of paleoclimate reconstructions than do the assignments of climate values to the surface sample reference sites. As such, the climate assignments reported can be expected to provide an empirically sound basis for paleoclimate reconstruction from fossil pollen samples developed in the study region.

The quality of the modern reconstructions in this study is comparable to that obtained in other studies in Europe and northeastern North America by entirely different multivariate methods (Guiot 1990; Bartlein and Whitlock 1993; Seppä and Birks 2002). The relatively lower precision for precipitation reconstruction is also seen in other data sets (Bartlein and Whitlock 1993; Peyron et al. 1998; Davis et al. 2000), and reflects the heterogeneity of the precipitation-vegetation relationship in the surface sample set. Overall, the results of the validation tests indicate that the reconstruction procedure can be confidently applied to Holocene fossil pollen data from the southern California montane region. In particular, when selection of analogs is largely confined to the montane conifer forest group, average absolute anomalies of $<2°$ for temperature, $<10\%$ for apparent elevation, and $<12\%$ for precipitation can be expected. In cases of selection of analogs with mixed representation across vegetation categories (e.g., conifer-dominated forests and conifer-oak forests), constraining analog selection according to the criteria described above and in Wahl (2003) could be considered to achieve the most accurate results.

The congruence of results between this study and those reported in Wahl (in press) in terms of best-performing cutoff values and the asymmetry in degradation of performance on either side of the range of best cutoffs is of particular interest, and has important implications beyond the validation of paleoenvironmental reconstruction methods in the study region. Up to this time, the primary focus for evaluation of appropriate cutoff values in implementations of the MAT with dissimilarity metrics (such as SCD) has been the reduction of false positive analogies (in terms of the vegetation characteristics associated with the pollen samples), which now appears to have been a bias that entails significant risk of "throwing out" relevant climate and vegetation reconstruction information via too-low cutoffs (cf. Wahl in press). The method used in this

paper of systematically varying the cutoff level when validating environmental reconstruction calibrations can be an important tool in determining analog identification thresholds that recover maximal climate and apparent elevation information from pollen samples. This method can be readily implemented with existing sample-site climate information, without the need for time- and labor-intensive effort to develop the site-specific vegetation data necessary to examine best-performing cutoffs in terms of distinguishing like from non-like vegetation.

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APPENDIX 1

The weighting scheme used for calculating precipitation values for samples 7, 8, 9, and 12 was developed to account for the lack of nearby precipitation-elevation equations for these four samples, and since the nearest instrumental data (from the Big Bear Lake station) suggest a localized precipitation-shadow effect (cf. the precipitation value assigned to sample 13). The *California Annual Precipitation* map (1999) isohyets are consistent with this interpretation.

The weights used were developed taking into account the following information: a) the annual precipitation value at the Lake Arrowhead reporting station is nearly identical to that interpolated at the lake by the map (103.8 cm from the instrumental data vs. 101.6 cm, or 40 inches, from the map); and b) the annual precipitation from the map for a high-elevation endpoint on San Bernardino Mountain is also 40 inches. With the elevations of the

Lake Arrowhead and San Bernardino Mountain endpoints used as bracketing values, two intermediate elevations were determined: a) for the location nearest samples 8, 9, and 12 that is transected by the 40-inch isohyet in the map; and b) for the location nearest sample 7 that is transected by the 40-inch isohyet. The relationships between these elevations and the elevations of the Lake Arrowhead and San Bernardino Mountain endpoints were used to determine the weights employed in the precipitation calculations.

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY ANNUAL BANQUET

Saturday, February 21, 2004 at the
Presidio Trust Log Cabin, San Francisco

Tour of Presidio: 1–3 p.m.
Reception: 5:30 p.m.
Dinner: 6:30 p.m.
Lecture: 8:00 p.m.

Dr. Harold Mooney
Professor, Department of Biological Sciences, Stanford University
"A personal view of California plant ecology: past, present and future"

Dinner and beverages: $35 non-student, $20 student

For further information, please contact
Dr. Mark Brunell, mbrunell@uop.edu;
(209) 946-7479; (209) 946-3022 fax.

POLLEN SURFACE SAMPLES FOR PALEOENVIRONMENTAL RECONSTRUCTION FROM THE COAST AND TRANSVERSE RANGES OF SOUTHERN CALIFORNIA

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ABSTRACT

Modern pollen assemblages from forty-one sites in the southern California cismontane region are described, which serve as a modern analog reference set for developing Holocene paleoenvironmental reconstructions from fossil pollen sites in the mountains east of Los Angeles and San Diego. The reference assemblages are derived from soil surface samples. The pollen characteristics of the samples are described in detail, organized according to the major vegetation types occurring in the southern California mountains and nearby cismontane foothill regions. The characteristics of the samples in terms of their patterns in multivariate taxon space (using the squared chord distance, SCD) are also described, which demonstrate that that the major vegetation types can be successfully distinguished by their pollen using the SCD, with some overlap across types that share dominant plant taxa. Threshold values of pollen representation and ratios of the pollen proportions of important taxa are shown to be useful refinements to the SCD information to help distinguish between samples from overlapping vegetation types. The overall quality of the sample set is found to be well-suited for the purpose of paleo-reconstruction of past climate and vegetation at regional montane fossil sites.

Key Words: southern California, pollen, surface samples, palynology, paleoecology, paleoclimate, modern analog technique.

Pollen assemblages from the sediment surfaces of lakes and small forest hollows, from moss polsters, and from the soil surface in small clearings in vegetation are commonly used to develop reference sets of the modern pollen "rain" characteristic of particular kinds of vegetation (e.g., Maher 1963; McAndrews and Wright 1969; Overpeck et al. 1985; Anderson and Davis 1988; Anderson et al. 1989; Davis 1995; Calcote 1998; Minckley and Whitlock 2000; Anderson and Koehler 2003). These sets of "surface samples" are often compared with fossil pollen assemblages preserved in lakes, bogs, forest hollows, and mountain wet meadows with the goal of reconstructing the vegetation that produced the fossil assemblages (e.g., Maher 1972; Overpeck et al. 1985; Anderson et al. 1989; Anderson 1990; Anderson and Smith 1994; Davis et al. 1998; Davis 1999). When used this way, particular surface samples are called "analogs" when they closely match a fossil pollen assemblage, and the vegetation that produced the fossil pollen is assumed to be similar to the modern vegetation at its analog sites (Overpeck et al. 1985; Calcote 1998; Davis et al. 1998). Conversely, a fossil pollen sample is said to be a "no analog" assemblage if it does not match any surface sample closely (Overpeck et al. 1985; Calcote 1998).

This analog method is often extended by the assumption that the climate associated with a particular surface sample site is a major factor determining the vegetation at the site. Thus, the assumed likeness of ancient and modern vegetation for an analog situation can be interpreted to imply a similar closeness of ancient and modern climates (e.g., Overpeck et al. 1985; Anderson et al. 1989; Guiot et al. 1989; Guiot 1990; Bartlein and Whitlock 1993; Anderson and Smith 1994; Peyron et al. 1998; Davis 1999; Davis et. al. 2000). This technique of comparing modern and fossil pollen assemblages to reconstruct past climates and vegetation is termed the "modern analog technique" or MAT (Bartlein and Whitlock 1993; Davis 1995; Calcote 1998; Davis et al. 1998), as distinguished from other quantitative reconstruction strategies such as "transfer functions" and "response surfaces", which associate modern and fossil pollen assemblages directly with climate parameters via regression equations and other mathematical fitting techniques (e.g., Webb and Bryson 1972; Bryson and Kutzbach 1974; Bernabo 1981; Howe and Webb 1983; Bartlein et al. 1984; Bartlein and Webb 1985; Bartlein et al. 1986; Prentice et al. 1991; Bartlein and Whitlock 1993; Webb et al. 1993; Bartlein et al. 1998).

The work presented in this paper describes a new surface sample set from the cismontane region of southern California (west of the eastern, desert crest of the coastal mountains; Fig. 1), whose purpose is to provide calibration data for climate and vegetation reconstructions from fossil pollen sites in the

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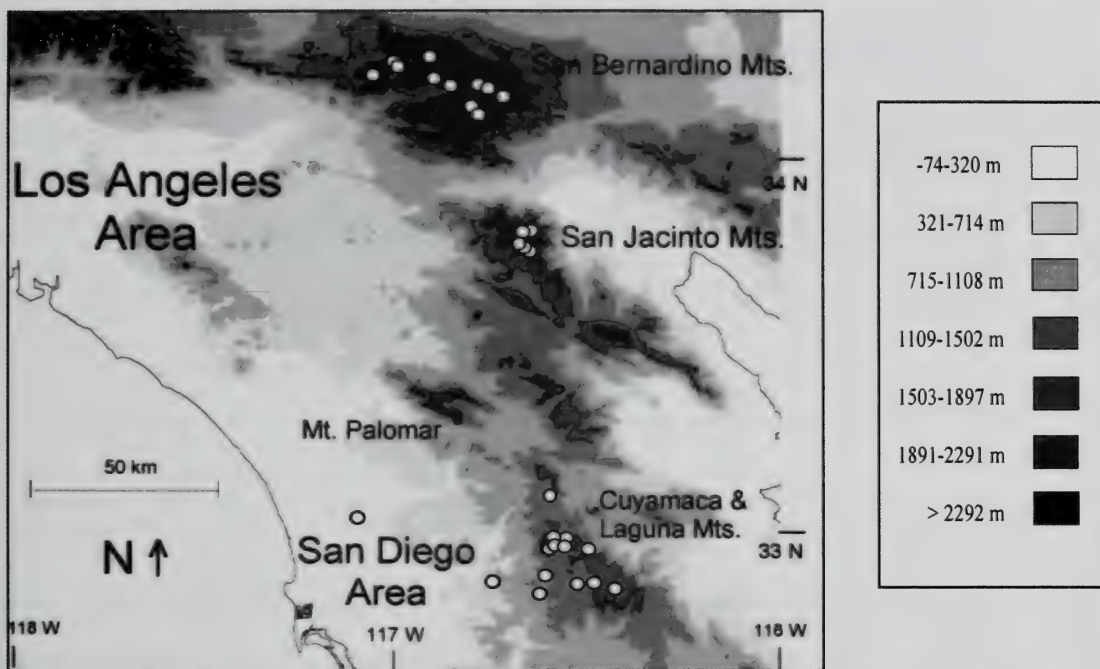
FIG. 1. Digital elevation map of southwestern California, U.S.A. Surface sample sites used in this study are shown as white dots. Contour lines are shown at sea level and 1500 m elevations. Dark gray-to-black shaded polygons approximately represent regional montane areas (>1500 m; max. elevation, 3474 m). Source data and elevation ranges for the DEM base map are from the United States Department of the Interior, Geological Survey.

region's Coast and Transverse Ranges (Wahl 2002; E. Wahl, Holocene paleoenvironmental reconstruction in the southern California Peninsular and Transverse Ranges, *in preparation*). The pollen representation of these samples is examined in two complementary ways: a) the pollen taxonomic characteristics of the samples are described and related to regional vegetation and climate characteristics; and b) the relationships among the samples are analyzed in terms of a multivariate distance metric commonly used for analog selection with pollen and other microbiological data (squared chord distance (SCD); Overpeck et al. 1985). The pollen/vegetation relationships of samples of special interest are examined in Appendix 1. The general issue of appropriate levels of SCD closeness for determining analogs is treated in Wahl (in press).

METHODS

Field Methods

Forty-one sites were sampled in the San Bernardino, San Jacinto, Cuyamaca, Laguna, and Palomar Mountains of southern California during 1996–1998 (Table 1, Fig. 1). Five to ten samples of sediment from the interface of the humus and underlying soil, or of the top few centimeters of the soil surface when humus was absent or not well developed, were collected within a radius of 20–40 m at each site, following the methods of Adam and Mehringer (1975). Sampling was typically done in small to large openings (20–200 m across) in the vegetation canopy, or in a few cases in the understory of relatively open forests. This criterion was applied so that the sample sites would mimic as much as possible the pollen deposition characteristics of the wet meadows from which fossil pollen samples have been extracted (Wahl 2002). It is recognized that this mimicry is exclusive of pollen from vegetation restricted to the hydric meadow environments, which is taken into account in quantitative and qualitative comparison of the fossil and surface pollen assemblages. In the cases of the three mixed chaparral samples and the coastal sage scrub sample, the samples were taken in smaller openings (3–10 m across) and two to four adjacent openings were included in each case.

The samples cover the range of widely-occurring vegetation types in the mountain and adjacent locations of the study area, including: montane conifer forest and woodland; mixed conifer-oak forest and woodland; oak woodland; manzanita chaparral (dominated by *Arctostaphylos* spp); chamise chaparral (dominated by *Adenostoma fasciculatum*); mixed chaparral (including *A. fasciculatum, Rhus* spp., *Rhamnus* spp., *Quercus* spp., *Arctostaphylos* spp., *Ceanothus* spp., and other shrubs); sagebrush (*Artemisia tridentata*)-pine steppe; and coastal-area

TABLE 1. SURFACE SAMPLE SITES. Vegetation characterizations follow the usage of Munz (1974), Thorne (1988), and Hickman (1996). "Jeffrey", "Limber", and "Lodgepole" in the conifer-dominated forest group are common names of important regional pine species. The botanical names are *Pinus jeffreyi, P. lambertiana,* and *P. contorta* subsp. *murrayana,* respectively. Other botanical names are given in the text.

Sample	Main vegetation category	Latitude			Longitude			Elevation (m)
		Deg	Min	Sec	Deg	Min	Sec	
	Upper & Mid-Montane Conifer-dominated Forests (1–20)							
1	Lodgepole/Jeffrey/Fir Forest	34	12	10	116	46	55	2774
2	Western Juniper/Lodgepole Forest/Woodland	34	12	0	116	45	53	2746
3	Fir/Lodgepole Forest	34	12	4	116	45	57	2707
4	Fir/Limber/Juniper Woodland	34	12	30	116	51	19	2597
5	Fir/Jeffrey/Lodgepole Forest	34	7	21	116	46	51	2499
6	Jeffrey/Fir Forest	34	7	29	116	46	56	2481
7	Pine/Fir/Oak Forest	34	14	6	117	3	7	2243
8	Pine/Fir Forest	34	15	58	117	0	21	2228
9	Pine/Fir Forest	34	16	5	117	0	22	2228
10	Pine/Western Juniper/Fir Forest	34	10	20	116	43	4	2438
11	Lodgepole/Limber Forest	33	48	2	116	40	21	2926
12	Pine/Fir Forest	34	13	19	116	53	58	2402
13	Pine/Fir Forest	34	16	53	116	54	51	2286
14	Lodgepole/Fir Forest	33	48	24	116	39	12	2682
15	Fir/Pine Forest—Aspen Grove (> dense with Aspen)	34	8	54	116	47	59	2170
16	Fir/Pine Forest—Aspen Grove (< dense with Aspen)	34	8	54	116	47	49	2170
17	Pine/Fir/Oak/Cedar Forest	32	56	56	116	36	16	1890
18	Pine/Alder/Fir Forest	33	46	9	116	39	44	2405
19	Pine/Fir Forest	33	46	9	116	39	44	2405
20	Pine/Fir Forest	33	46	9	116	39	44	2402
	Lower-Montane Conifer-Oak Forests, Meadows, Chaparral (21–33)							
21	Manzanita Chaparral	32	56	38	116	29	28	1692
22	Pine/Oak Forest	32	50	15	116	25	24	1829
23	Oak/Conifer Forest	34	8	5	116	58	56	1682
24	Cedar/Pine/Oak/Fir Forest	32	57	15	116	35	16	1573
25	Pine/Oak Forest	32	51	9	116	28	56	1554
26	Oak/Cedar/Pine Forest	32	58	2	116	35	8	1451
27	Oak/Cedar Stand-in Pine/Oak/Cedar/Fir Forest	32	58	10	116	35	1	1448
28	Pine/Oak Open Forest Clearing	32	58	15	116	34	26	1439
29	Oak/Pine Forest	33	5	22	116	35	40	1228
30	Cedar/Oak/Fir Forest—Burn Site	33	20	13	116	54	27	1573
31	Meadow-in Pine/Oak/Cedar/Fir Forest	32	58	8	116	35	4	1439
32	Meadow-in Pine/Oak/Cedar/Fir Forest	32	58	6	116	35	5	1434
33	Mixed Chaparral—Mt. Mahogany dominated	32	56	58	116	33	35	1384
	Steppe, Mixed Chaparral, Oak Woodland (34–39)							
34	Sagebrush Steppe (> open phase)	32	51	2	116	31	17	1132
35	Sagebrush Steppe (> closed phase)	32	51	5	116	31	22	1125
36	Oak Woodland (> closed phase)	33	17	28	116	50	2	1414
37	Oak Woodland (> open phase)	32	49	9	116	37	7	1073
38	Mixed Chaparral	32	52	9	116	36	29	1091
39	Mixed Chaparral	32	49	21	116	37	17	1061
	Chamise Chaparral Sage scrub							
40	Chamise Chaparral	32	51	21	116	44	30	817
41	Coastal Sage Scrub	33	1	49	117	5	34	244

sage (*Artemisia californica*) scrub. Two lower-montane meadow samples and a sample from a recently burned site in conifer-oak forest were also included for additional calibration. This coverage was designed to include vegetation types both within and beyond the probable range of vegetation that occurred during the Holocene surrounding the wet meadow fossil sites—based on both the modern vegetation/climate relationships in the region (Munz 1974; Thorne 1988; cf. companion paper, Wahl 2003) and the range of climate change from late-glacial to modern times in nearby portions of the Southwest, as determined by paleoecological records and comparisons of paleo-data with climate model simulations (cf. Thompson et al. 1993; Bartlein et al. 1998). The characterizations of the vegetation types follow Munz (1974), Beauchamp (1986), and Thorne (1988), and are based on the percentage cover of plant taxa at each site, documented in Wahl (2002). All scientific names for plants conform to those in Hickman (1996).

Laboratory Methods

The samples were prepared according to standard chemical methods for extracting pollen from sediments (Faegri and Iversen 1989; E. Cushing, *personal communication*), modified according the characteristics of the specific samples in this study. These modifications were: a) each sample was initially dispersed in a 5% solution of sodium pyrophosphate and sieved through 120 μm and 8 μm mesh screens to remove coarse and fine debris; b) a hot KOH bath was used only on samples from the humus/soil interface; c) HCl acid wash was not used since these samples do not contain carbonates; and d) HF acid bath was not used on samples with little mineral content. A known concentration of exotic *Lycopodium* spores was added to each sample so that pollen concentrations could be calculated.

The samples were counted at 200× to 1000× magnification. 300–400 grains were counted for most samples; four samples had between 400 and 700 grains and in two samples 240–300 grains were counted. Reference pollen came from the collection of the University of Minnesota Herbarium (code designation MIN), and from the personal collections of M. B. Davis, K. L. Cole, and E. Wahl. Rules for summing *Pinus* (pine), *Abies* (fir), and Pinaceae-undifferentiated fragments are described in Wahl (2002). Unidentifiable pollen was characterized as degraded, crumpled, broken, corroded, or obscured, following the usage of E. Cushing (*personal communication*).

In Figure 2, the "Other Asteraceae" category includes all pollen of the *Ambrosia* tribe, along with Tubuliflorae-undifferentiated and Liguliflorae-undifferentiated pollen. The "*Rhus/Toxicodendron*" category also includes the pollen of *Malosma laurina* (laurel sumac), a characteristic species of the coastal sage scrub also known as *Rhus laurina*

(Munz 1974; Hickman 1996). With the exception of *Pinus,* where a genus name is given without a specific epithet, it means that pollen grains of species within the genus are not reliably distinguishable with standard identification techniques. Several individual species and groups of species of *Pinus* within the study region have pollen that is distinguishable, with allowance for intermediate and indeterminate characteristics (Wahl 2002). However, in Figure 2 and the analysis of SCD's between the samples, *Pinus* is reported as a single type since most pine grains counted were either indeterminate or of the mixed *Pinus ponderosa/jeffreyi/coulteri* type and since few *Pinus* grains can be distinguished to sub-generic categories in the fossil pollen record for which these surface samples are used as an analog set.

The *Abies* pollen in these samples almost certainly comes from the species *Abies concolor* (white fir), which is the only native fir growing in the region (Munz 1974). No non-native firs were noted at or near any of the sample sites. The Cupressaceae-undifferentiated pollen in these samples most likely comes from *Calocedrus decurrens* (incense cedar) at most forest sites, from *Juniperus occidentalis,* var. *australis* (western juniper, *sensu* Munz 1974) at forest/woodland sites 2, 3 and 10, and from western juniper and *Juniperus osteosperma* (Utah juniper) at woodland site 4. Incense cedar, western juniper, and Utah juniper were the only native members of the Cupressaceae family at or near their respective sample sites (Munz 1974), and no non-native members of this family were noted at or near these locations.

Quantitative Methods

Temperature and precipitation values for each sample were assigned from instrumental data (NOAA) and precipitation map data (*California Annual Precipitation* 1999) by deriving six elevation/temperature relationships and eleven elevation/precipitation relationships for the individual mountain ranges and portions of individual ranges (Wahl 2003). The instrumental data coverage is as spatially fine as possible given available data sources. The normative period of record is 1961–1990, other periods as close to this period as possible were used when the full range 1961–1990 was not available for a specific station. The names and locations of the instrumental stations, the specific elevation/climate functions, and deviations from the normative period of record are detailed in Wahl (2003).

The squared chord distance (SCD) used to examine similarity and dissimilarity between the surface samples in multivariate pollen-taxon space is defined by the formula:

$$SCD_{jk} = \Sigma_i(p_{ij}^{0.5} - p_{ik}^{0.5})^2;$$

where p is the pollen proportion (expressed in the range 0–1) of a taxon included in the comparison, i = 1 . . . n are the included pollen types, and j
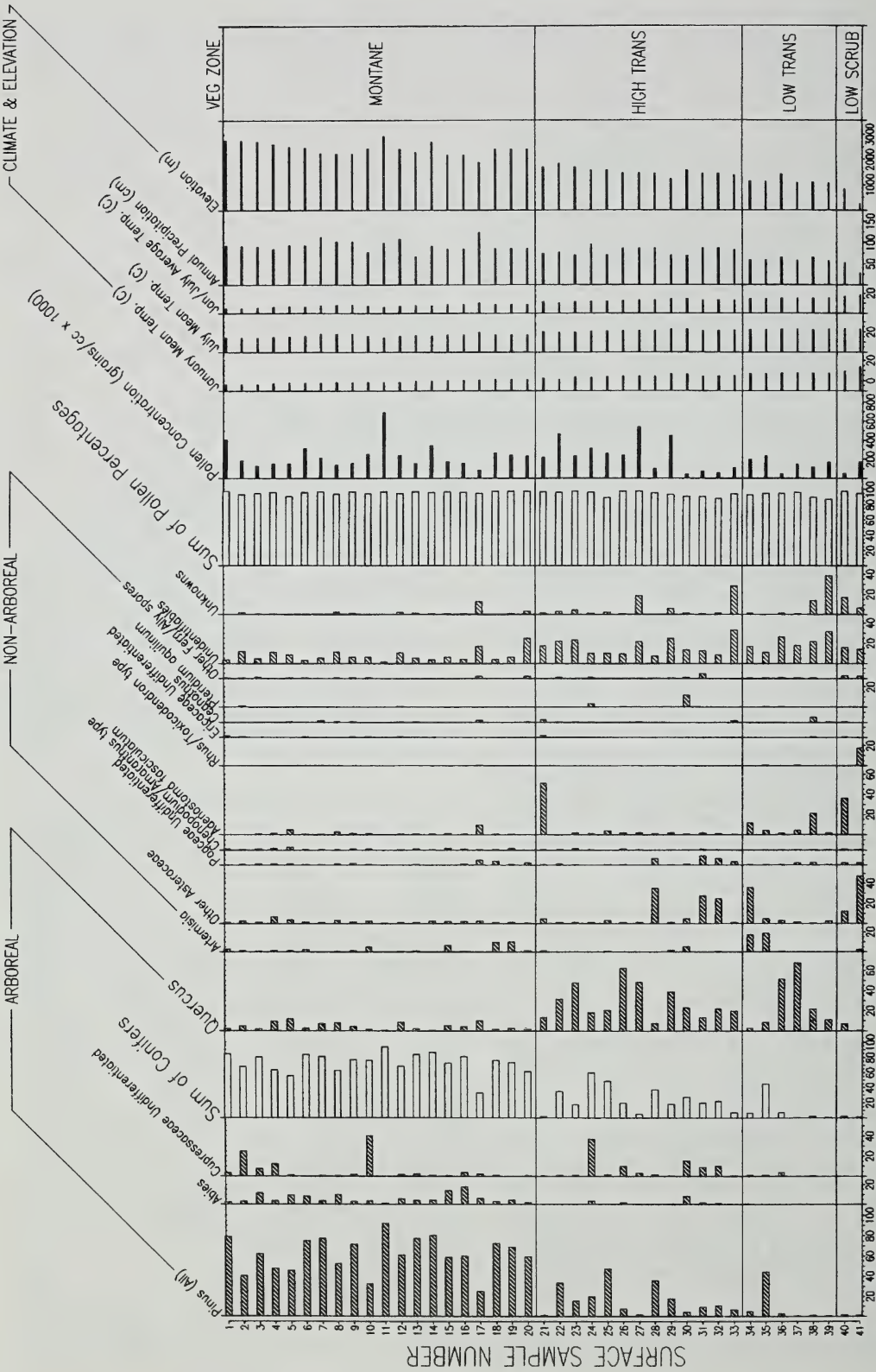
Fig. 2. Pollen diagram of surface samples. Sample numbering conforms to Table 1. Measurements on the horizontal axis are pollen percentages, except as defined otherwise. The term "High Trans" refers to the Lower-Montane Conifer-Oak Forests, Meadows, and Chaparral grouping in Table 1, sometimes called "high transition" vegetation in the region. The term "Low Trans" refers to the Steppe, Mixed Chaparral, and Oak Woodland grouping in Table 1, sometimes called "low transition" vegetation. The term "transition" (cf. Beauchamp 1986) refers to the lower montane and upper foothill areas of the region as a heterogenous zone of vegetation between the montane conifer-dominated forests and the scrub chaparral and coastal sage vegetation that dominates the lower foothill and coastal plain areas.

and k represent the two samples being compared (Overpeck et al. 1985). The entire range of the SCD is zero to two. The range of best SCD values that jointly select like vegetation sample comparisons as analogs and exclude unlike vegetation sample comparisons as non-analogs is ~0.20–0.27 for this set of samples. This range of best SCD "cutoff" values was determined using a new analytical method that jointly minimizes the occurrence of false positive comparisons (misidentification of samples from different vegetation types as being from the same type) and false negative comparisons (misidentification of samples from the same vegetation type as being from different types), described in Wahl (in press).

The range 0.20–0.27 is generally larger than results from related studies examining SCD cutoff values for analog selection in North America. Specifically: a) Overpeck et al. (1985) determined cutoffs of 0.15 and 0.12 for vegetation formations and forest types in eastern North America, respectively; b) Bartlein and Whitlock (1993) used a cutoff of 0.205 for north-midwestern/northeastern North America vegetation formations; c) Calcote (1998) determined a cutoff of 0.05 for forest stand types (spatially and vegetatively finer-scaled than the definitions used by Overpeck et al. and Bartlein and Whitlock) in northern Wisconsin and the Upper Peninsula of Michigan; d) Anderson et al. (1989) identified 0.095 as the cutoff for "good analogs"/"strong analogs" for grasslands, parklands, boreal forests, and tundra in interior Alaska and far northwestern North America, and identified 0.185 as separating "analog" from "no analog" situations; e) Oswald et al. (2003) determined a cutoff of 0.075 for two different kinds of tundra vegetation in Alaska; and f) Davis (1995) determined a cutoff of 0.15 for a variety of vegetation types in large portions of the western and southwestern United States. With the exception of Oswald et al., these studies focus primarily on the reduction of false positive errors and do not rigorously consider the concomitant loss of information resulting from false negative errors, which reduces the strict comparability of their results and those from the data set reported here. The results of several new studies (Gavin et al. 2003; Oswald et al. 2003; Wahl in press) demonstrate that appropriate analog cutoff levels can be expected to vary among surface sample sets from different regions with associated differences in vegetation, and thus should be separately examined for regionally-specific data sets.

The taxa included in the SCD calculations are the same as those shown in the pollen diagram in Figure 2. The *Ceanothus* and *Chenopodium/Amaranthus* pollen types and the "Other Fern/Ally" spore category are summed together with the unknown and unidentifiable categories in the calculations. This grouping adds together the least represented non-arboreal pollen and spore types (with the exception of the Ericaceae-undifferentiated tax-

on, which in this region is largely associated with manzanita chaparral) with the unidentifiables and unknowns to form a generic category of largely non-arboreal pollen. Categorizing unknown and unidentifiable pollen as largely non-arboreal is justified based on experience in pollen counting, in which the pollen types of all the regional trees are known and the only kind of arboreal pollen that may have been included in the unidentifiable category due to poor preservation is *Quercus* (oak). (Poorly-preserved material with some resemblance to *Pinus, Abies, Alnus* (alder), *Populus* (cottonwood/aspen), or Cupressaceae-undifferentiated pollen either was positively identifiable as one of these types or could not be definitively considered to be pollen.) The possible *Quercus* grains that were included in the unidentifiable category are generally much less than 30% of the total unidentifiable pollen; the exceptions are in samples with otherwise high levels of *Quercus* pollen. At least, the combined, largely non-arboreal category represents pollen that is not from coniferous trees. Since the distinction between conifer-dominated forests and other kinds of vegetation in the region is the single most important characteristic of the pollen record in this study, including the unidentifiables and unknowns in this way preserves useful information. The proportions of the included categories were calculated on the basis of the sum of included pollen and spores, which is standard practice in calculating SCD (Calcote 1998). Due to idiosyncratic biases in the pollen representation characteristics of sample 17 (montane conifer forest on Mt. Cuyamaca), caused by site-specific orographic and vegetation factors (Wahl 2002), the *Adenostoma fasciculatum* and *Ceanothus* pollen types were excluded from the pollen sum of this sample in calculating the SCD's.

<center>RESULTS</center>

The location, elevation, and type of vegetation for each surface sample are listed in Table 1. Pollen percentages of the samples for 14 taxonomic categories, along with unidentifiable and unknown pollen, are shown in Figure 2; the pollen sum includes all pollen and fern/ally spores. The graphed categories account for over 90% of total pollen in 37 of the samples, and over 87% in the remaining four. The primary pollen count data are archived with the North American Pollen Data Base and are accessible on the World Wide Web at *http://www.ngdc.noaa.gov/paleo/pollen.html*. Figure 2 also gives January (monthly mean) temperature, July (monthly mean) temperature, average January and July temperature, and annual precipitation for each surface sample site. Average January and July temperature is included as an approximation of annual temperature, at the scale of resolution available in some paleoclimate model experiments that have been extensively compared to
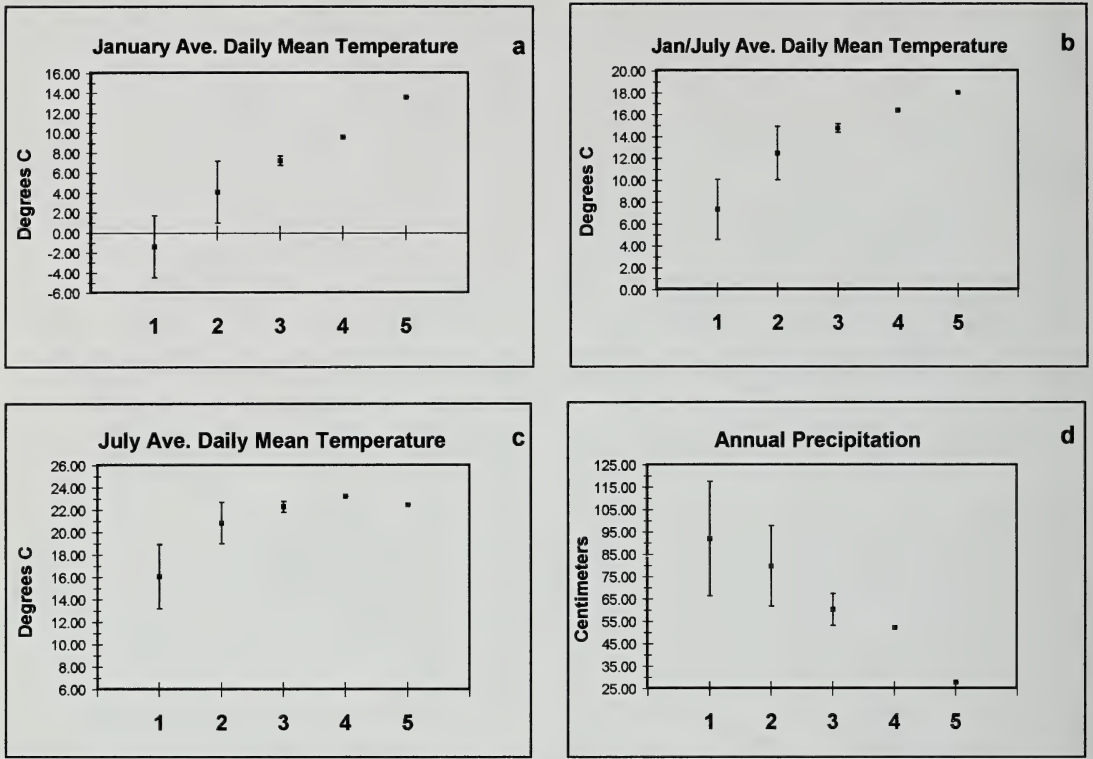
Fig. 3. Climate ranges of vegetation categories. Categories conform to Table 1 and Figure 2: 1) Upper- and Mid-Montane Conifer-dominated Forests; 2) Lower-Montane Vegetation; 3) Steppe, Mixed Chaparral, and Oak Woodland; 4) Chamise Chaparral; and 5) Coastal Sage Scrub. Data points and error bars for 1–3 show the mean and 2× standard deviation for all samples in the category. Data points for 4–5 show the value for the one sample in the category.

North American paleoclimate data (COHMAP members 1988; Thompson et al. 1993). The average values and ranges of variation of the climate variables, organized by vegetation category, are shown in Figure 3.

Vegetation of the Samples in Association with Temperature and Precipitation

The vegetation at the sample sites corresponds closely with an elevation-related temperature gradient (higher elevation/lower temperature), and similarly, but somewhat less closely, with an elevation-related precipitation gradient (higher elevation/higher precipitation) (Figs. 2, 3). These correspondences are commonly noted in the botanical and ecological literature of the region (Munz 1974; Beauchamp 1986; Thorne 1988), and are validated independently here by determination of climate values specific to each sample site (Wahl 2003). The samples span an approximately continuous range of elevations between 800–2800 m, along with one near-coastal site at 244 m; they represent eleven vegetation types, which in turn can be aggregated into five broader vegetation categories (Table 1, Fig. 2). The categories and vegetation types include: 1) mid- and upper-montane conifer-dominated forests and woodlands; 2) lower-montane conifer-oak forests, meadows, and relatively cool-temperature manzanita and mixed chaparrals; 3) lower-montane and foothill sagebrush-pine steppe, oak woodlands, and relatively warm-temperature mixed chaparrals; 4) foothill chamise chaparral; and 5) low-elevation coastal sage scrub.

The vegetation categories, and types within each category, correspond most closely with the gradient of January temperature (Fig. 3) (Wahl 2003). Thus, in Table 1 and Figure 2 the samples are arranged in a nested order according to: a) average January temperature of the five categories, b) average January temperature of the vegetation types within each category, and c) January temperature of the individual samples within each vegetation type.

Pollen Characteristics of the Samples

Montane conifer forests and conifer-oak forests. The most salient characteristic of the pollen data is the distinction between the montane conifer-dominated forests/woodlands and the rest of the samples. This distinction is evident in the fourth and fifth columns of the percentages in Figure 2, which

show the sum of conifer pollen and *Quercus* pollen, respectively. The sharp switch from very little *Quercus* pollen in the montane coniferous forests to much greater percentages in many of the lower-montane and foothill samples closely parallels the presence/absence of oak trees and shrubs in the regional vegetation (cf. Munz 1974; Thorne 1988; Roberts 1995).

Specifically, samples from the relatively cooler, wetter conifer-dominated forests (1–20) can be readily distinguished from the relatively warmer, drier mixed conifer-oak forests (22–30) by the percentage of *Quercus* pollen in each forest type. In the samples reported here, *Quercus* pollen never exceeds 11.5% in the montane conifer-dominated forests and always exceeds 18% in mixed conifer-oak forests, with one exception. The exception is sample 28, from a relatively large opening (~60 m diameter) in mixed pine-oak forest; *Quercus* pollen representation would be 12.5% in this sample if the large percentages of Other Asteraceae and Poaceae-undifferentiated (grass) pollen that come from plants confined to the opening were eliminated. This distinction in pollen representation between forest types is strongly consistent with the pollen spectra reported from other California surface samples. *Quercus* pollen always exceeds 19% in mixed conifer-oak forests and never exceeds 9.5% in conifer-dominated forests (with one exception, discussed below) in the only other reported surface sample network from southern California (Anderson and Koehler 2003), and it averages 18% in "xeric forests" and 8% in "mesic forests" sampled between 34° and 38°N (Davis 1995). Moreover, the higher representations of *Quercus* pollen in Davis' samples are associated with annual precipitation between 50–90 cm, a range similar to (but extending lower than) that of the conifer-oak forest samples reported here (Fig. 2; Table 3 in Wahl 2003). Adam and West (1983) demonstrate a similar relationship between elevation and *Pinus/Quercus* pollen representation for the area near Clear Lake in northern California, which they use to calibrate climate reconstructions over the last 128,000 years. Within the conifer-oak forests, the relative dominance of conifers and oaks in the vegetation is reliably reflected by the relative proportions of conifer and *Quercus* pollen in the surface samples: a conifer pollen/*Quercus* pollen ratio greater than one (>1) signifies a forest with more conifers than oaks, whereas a ratio less than one (<1) signifies a forest with more oaks than conifers.

Characteristics of conifer pollen representation for the surface samples in and near the fossil meadow sites are described in Appendix 1.

Chaparral, steppe, oak woodland, and sage scrub vegetation. The chaparral (21, 33, 38–40), steppe (34, 35), oak woodland (36, 37), and coastal scrub (41) samples are characterized generally by very low percentages (<6.5%) of *Pinus* and other conifer pollen, and by significant percentages of pollen from plants specific to each site's vegetation. The low *Pinus* pollen levels, even in vegetation relatively near forest with significant proportions of pine, are consistent with the results of Anderson and Koehler (2003), and with observations from nearby northwestern Mexico (Orvis 1998), the American Sonoran Desert (Hevly et al. 1965), and other parts of California (Davis 1995). For example, the highest pine pollen recorded in this group, 6.3%, is in sample 33, less than 2 km in the prevailing downwind direction (E and SE) from extensive pine-oak forest. Exceptions to these general characterizations are exhibited by: a) sample 21, which has a nearly mono-specific cover of manzanita shrubs, and yet has <2% Ericaceae-undifferentiated pollen (insect-pollinated) along with 51% *Adenostoma fasciculatum* pollen (wind-pollinated)–presumably from chamise plants at the fringe of the site; b) sample 33, which is a "cool" mixed chaparral dominated by *Cercocarpus betuloides* (mountain mahogany), and yet has <2% *Cercocarpus* pollen (presumably insect-pollinated); and c) sample 35, which was taken in a small pine stand within sagebrush-pine steppe and has 44% *Pinus* pollen–contrasting sharply with sample 34 (~200 m away in more open steppe with no pines), which has nearly the same proportion of *Artemisia* pollen as sample 35, but <5% *Pinus* pollen and a very high percentage of Other Asteraceae pollen (reflecting the plant cover between the sagebrush plants).

Unknown and unidentifiable pollen. The highest values of unknown pollen in this set occur in three chaparral samples (33, 39, and 40) and in an oak-cedar stand surrounded by conifer-oak forest (27). The highest values of unidentifiable pollen also occur in the non-forested samples (esp. 33 and 39), along with some high values in the conifer-oak forest samples (22, 23, 27, and 29) and a high value in one conifer forest sample (20). The high levels of unidentifiable pollen reflect the one significant disadvantage of using soil surface samples; biological activity within the soil and oxidative weathering in the aerobic conditions of the soil surface can lead to degradation in pollen preservation (Davis 1995; Orvis 1998). However, since the surfaces of the wet meadow fossil sites used in the paleo-reconstruction portion of this research are much more akin to soil surfaces than they are to the surfaces of moss polsters (the other potential source of analog samples widely available in the region, cf. Anderson and Koehler 2003), it was decided that soil samples would provide the best analogs for the fossil samples. Moss polsters are also subject to biases of representation from overhanging and adjacent plants that soil samples collected according to the methods of Adam and Mehringer (1975) avoid (Davis 1995). The high unknown pollen values in the three chaparral samples noted are attributable to: a) conservative identification criteria—a notable ex-
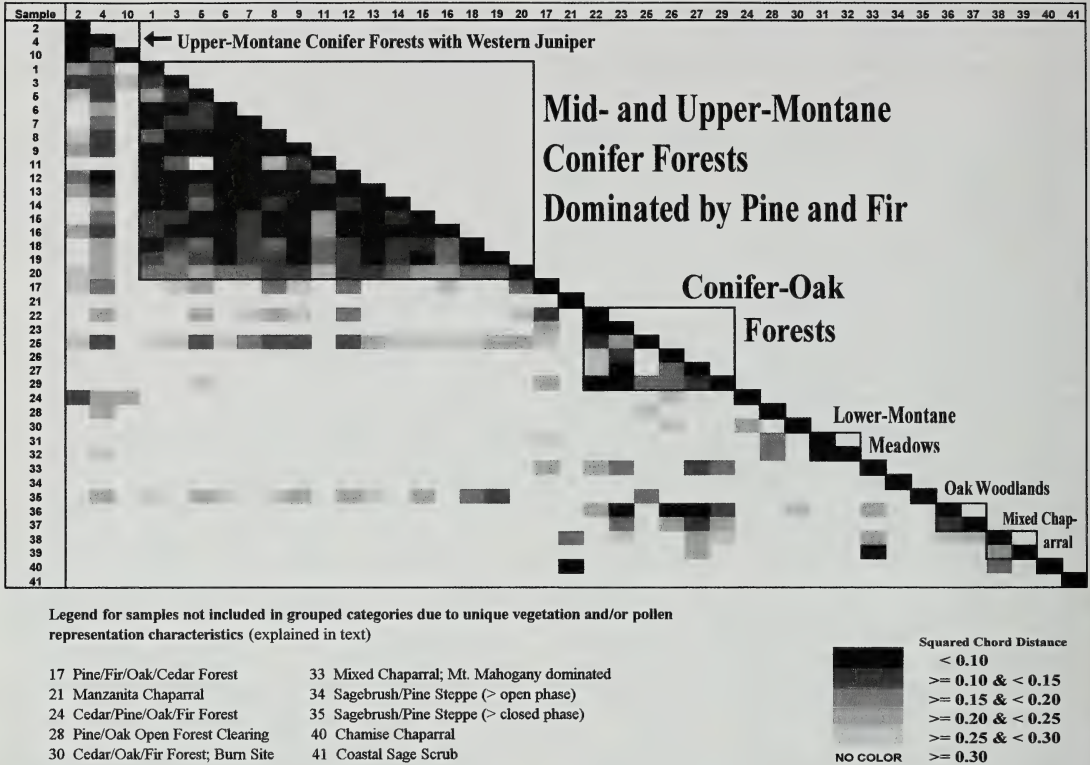
FIG. 4. Pair-wise comparison of southern California surface samples in terms of squared chord distance (SCD) dissimilarity metric. The numbers along the axes are the identification numbers of the samples from Table 1 and Figure 2, in the same order for each axis. Each cell along and below the diagonal indicates the SCD between two samples; for example, the values along the diagonal are all in the lowest (black) ranking, since these cells compare each surface sample to itself and thus have a dissimilarity value of zero. The sequence of the samples in Figure 4 varies slightly from the temperature ordering of Table 1 and Figure 2, in order to group together the three montane conifer forest/woodland samples with significant cover of western juniper (2, 4, and 10) and distinguish forest samples 17, 24, and 28, which have unique pollen-representation characteristics (Fig. 2). The heavy-outline boxes indicate comparisons between samples from similar vegetation. From upper left to lower right, these groups include: a) the three forest/woodland samples with significant cover of western juniper; b) all other samples from the montane conifer-dominated forests, with the exception of sample 17 (placed immediately after this group); c) the mixed conifer-oak forest samples, with the exception of samples 24 and 28 (placed immediately after this group); d) the two lower-montane meadow samples; e) the two oak woodland samples; and f) the two mixed chaparral samples. Samples not included in the outlined groups have relatively unique pollen characteristics, and are best considered separately for the purpose of examining the SCD's.

ample is a tricolporate type that might be immature *Adenostoma fasciculatum* pollen, but which could not be conclusively identified as such; b) the high heterogeneity of the vegetation at the mixed chaparral sites; and, to a lesser extent, c) the lack of a comprehensive manual for the pollen of the western United States (cf. Davis 1995). Combined values of unidentifiable and unknown pollen are greater than 33% in five samples (27, 33, 38, 39, and 40), and greater than 25% in ten samples (the five already listed plus 17, 20, 23, 29, and 36).

Similarities and Dissimilarities between Samples in Multivariate Space

Figure 4 shows the 861 possible comparisons among the 41 surface samples, in terms of the SCD's between the pollen assemblages. Based on determination of SCD threshold values that maximally distinguish within-group comparisons from outside-of-group comparisons (described above), pairs of samples with SCD's ≤ 0.25 are characterized as "similar" in the results below.

"Within-group" comparisons. The most important feature of the SCD comparisons is that the closest similarities (represented by the darkest shadings) generally occur within the like-vegetation groupings. The only significant weakening of this general pattern occurs in the conifer-oak forest group, reflecting the heterogeneity within this vegetation type. In particular, samples 26 and 27 have SCD's >0.25 with samples 22 and 25, reflecting the

significant differences in the relative dominance of pines (22 and 25) and oaks (26 and 27) at the sample sites.

"Outside-of-group" comparisons: conifer-dominated forests. Of the three conifer forest/woodland samples with significant cover of western juniper, two (2 and 4) are similar to a number of the samples in the main conifer forest group dominated by pine and fir, while the third (10) is not similar to any sample in this group at the 0.25 level. The number and closeness of analogs between these two groups is inversely related to the relative dominance of Cupressaceae-undifferentiated pollen in samples 2, 4, and 10. Because Cupressaceae-undifferentiated pollen in sample 4 is relatively low in relation to samples 2 and 10, this sample also shows similarity to lower-montane conifer-oak forests with relatively high *Pinus* pollen representation (samples 22, 25, and 28). The likeness between samples 4 and 28 in terms of *Quercus* and unidentifiable pollen representation also helps offset the difference between them in the Other Asteraceae category. Forest sample 24 with abundant incense cedar pollen also has low SCD's with samples 2, 4, and 10.

The most notable characteristic of the outside-of-group similarities for the block of conifer forests dominated by pine and fir is how sharply this group is distinguished from the other vegetation types. Along with the similarities with samples 2 and 4 noted above, the forests in this block have similarities with only four other samples: 17, 22, 25, and 35. The similarities between the main group of conifer forests and samples 22 and 25 reflect the high *Pinus* pollen values of the latter two samples in relation to the other conifer-oak forests. The SCD similarities between several of the conifer-dominated forests (including sample 4) and sample 35 (sagebrush-pine steppe) are driven by the anomalously high percentage of *Pinus* pollen in sample 35.

Along with the similarities it has with the other conifer-dominated forests, sample 17 is also similar to three samples in the conifer-oak forest group (22, 23, and 29), due to its relatively low percentage of *Pinus* pollen and relatively high percentage of *Quercus* pollen in relation to the other conifer-dominated forests. The similarity between sample 17 and mixed chaparral sample 33 also is related to the relatively low *Pinus*/high *Quercus* pollen representation of sample 17, and to its relatively high percentage of unknown pollen.

"Outside-of-group" comparisons: conifer-oak forests. Along with the similarities it has with the conifer-dominated forests, the block of conifer-oak forests has expectable similarities with the oak woodland samples (36 and 37). Forest sample 27 is similar to the three mixed chaparral samples (33, 38, and 39), due to significant *Quercus* pollen from scrub oaks in the chaparral, along with the low lev-

els of *Pinus* and high levels of unidentifiable and unknown pollen shared by these samples. Three of the other conifer-oak forest samples (22, 23, and 29) also are similar to sample 33 because of the high *Quercus* and unidentifiable pollen common to these forest samples.

The similarities between sample 28 and lower-montane meadow samples 31 and 32 are expectable, since sample 28 is from a relatively large forest opening (~60 m diameter) in the same kind of conifer-oak forest matrix as samples 31 and 32. In these comparisons, high levels of Other Asteraceae pollen compensate for the differences in *Pinus* pollen representation between sample 28 and the meadow samples.

"Outside-of-group" comparisons: chaparral, steppe, oak woodland, and sage scrub vegetation. Manzanita chaparral sample 21 has similarities with chamise chaparral sample 40 and mixed chaparral sample 38. These relationships result from the very low representation of Ericaceae-undifferentiated pollen and very high representation of *Adenostoma fasciculatum* pollen in sample 21.* The similarity between mixed chaparral sample 38 and chamise chaparral sample 40 is due to the high value of *Adenostoma fasciculatum* pollen in sample 38.

Along with the similarities it has with a number of conifer-oak forest samples, lower-montane mixed chaparral sample 33 has similar pollen proportions to the foothill mixed chaparral samples (38 and 39), resulting in low SCD's in these comparisons. These similarities are expectable since the mountain mahogany that dominates the vegetation of sample 33 is poorly represented in the pollen rain, and since these samples share high levels of unidentifiable and unknown pollen. The similarity between sample 33 and oak woodland sample 36 is driven by the damping effect of the "signal-to-noise" characteristic of the SDC metric (Overpeck et al. 1985), which diminishes the impact of the large differences in *Quercus* and unknown pollen percentages between these two samples.

DISCUSSION

Pollen Characteristics

The results presented demonstrate the ability of pollen surface samples to register vegetation differences in the southern California Peninsular and eastern Transverse Ranges. In particular, spurious representation of abundant producers (especially pines) that are not present in the vegetation (McAndrews and Wright 1969; Anderson and Da-

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* In general, it is not possible to discern the presence of manzanita chaparral by the SCD method in this sample set. The presence of Ericaceae–undifferentiated pollen above trace levels in fossil pollen spectra can probably be interpreted to represent a significant coverage of plants from this family around the fossil sample site.

vis 1988; Lynch 1996) is generally of little significance. The clear distinction between non-forested and forest samples in terms of conifer pollen representation, even when the non-forested vegetation is nearby and downwind from forest (sample 33), allows this conclusion to be drawn with confidence. The general lack of problematic pollen over-representation allows subtleties of differential sizes of forest openings to be registered by the relative abundances of dominant arboreal pollen types, in particular *Pinus,* as shown by the transect from meadow edge into surrounding forest at Taquitz Meadow and by the transition from smaller to larger openings near and in Hual Cu Cuish Meadow (Appendix 1). The data from Hual Cu Cuish further demonstrate that a relatively low representation of *Pinus* pollen (10–15%) is indicative of the adjacent presence (<0.5 km) of forest or woodland with significant numbers of pines, in sharp contrast to the pollen representation threshold for pine noted in significant portions of North America east of the Rocky Mountains (McAndrews and Wright 1969; Lynch 1996) and some other portions of western North America (Davis 1995).

The lack of problematic pollen over-representation is apparently due to the character of the region's montane forests as islands of "Sierran" vegetation surrounded by various kinds of scrub and oak woodland (Thorne 1988). The forest cover in the southern California mountains is vastly less extensive in comparison to the forests of the Sierra Nevada, the Rocky Mountains, and eastern North America (Burns and Honkala 1990); it is also just downwind from one of the world's largest regions of effectively zero pollen production, the northeastern Pacific Ocean. The fetch over which pollen of abundant arboreal producers can be entrained is thus orders of magnitude smaller in the study region than it is in some of the larger western mountain chains and the East. The clear distinction between forest and non-forested samples in terms of conifer pollen representation is strongly mediated by this relative absence of background pollen. Sample 17 near the upwind edge of conifer-dominated forest on the western scarp of Mt. Cuyamaca also demonstrates this impact clearly; its percentage of *Pinus* pollen is the lowest of all the montane conifer-dominated forests and it has anomalously high levels of pollen from upwind chaparral plants (Fig. 2). A related lack of background *Pinus* pollen also occurs in the Interior Valley region of Oregon (Minckley and Whitlock 2000), which is also associated with a relatively small upwind fetch over which *Pinus* pollen can be entrained.

The only other set of surface samples reported from the montane portion of southern California (Anderson and Koehler 2003, based on moss pollsters rather than soil samples) shows pollen representation of specific plant taxa and discrimination between vegetation types that are generally consistent with the results reported in this paper. One significant discrepancy between the results reported here and those reported by Anderson and Koehler occurs in the vicinity of Taquitz and Skunk Cabbage Meadows in the San Jacinto Mountains (samples 18–20 here; sample SJ-12 in Anderson and Koehler). These samples were all collected within ~2 km of each other, in a relatively homogenous mixed conifer forest (pine/fir) that does not contain oak trees or shrubs. In the results reported here, the pollen representation of samples 18–20 is typical of the monane conifer-dominated forests in both studies, with >55% *Pinus* pollen and <3% *Quercus* pollen. However, in Anderson and Koehler's study the sample from this forest has only 20% *Pinus* pollen and 26% *Quercus* pollen, a spectrum that would generally identify it with significant, even dominant, presence of oaks at the sample site. Since Anderson and Koehler report no representation of either arboreal or scrub oaks at the SJ-12 site, it is unclear what causes this discrepancy, especially because they also find generally low levels of background *Pinus* and *Quercus* pollen throughout the region. Overall, the primary differences between the results presented here and those of Anderson and Koehler are the inclusion in this study of a number of samples from the Cuyamaca, Laguna, and Palomar Mountains and nearby foothills in San Diego County and the elevated presence of unidentifiable pollen (Fig. 2), resulting from the use of soil surface samples. Since this kind of sampling most closely mimics the characteristics of the wet meadow fossil records for which this surface sample set provides analogs (cf. Davis et al. 1985; Wahl 2002), the fact that relatively high values of unidentifiable pollen do not degrade the quality of the samples' pollen/vegetation registration is a key validation of the use of these samples for paleo-environmental reconstruction.

Squared Chord Distance Patterns and Analog Relationships

The pattern of SCD relationships determined by the samples reflects the relative clarity of signal in the vegetation-pollen relationships in the region's mountains. The great majority of SCD relationships ≤0.25 are for comparisons of samples of like vegetation (Fig. 4). The overlaps between groups indicating inappropriate analogies fall into expectable patterns, largely determined by shared dominance of one of the region's two most important pollen types, *Pinus* or *Quercus.* The overlap between the mid- and higher-montane conifer-dominated forests and some conifer-oak forests reflects the high proportions of conifer pollen, especially *Pinus,* shared by these samples. The overlap between two of the three conifer-dominated forests with significant cover of western juniper and many of the other conifer-dominated forests also reflects the high proportions of *Pinus* pollen shared by these samples. The overlap between the conifer-oak forests and

oak woodlands reflects the high levels of *Quercus* pollen in both groups, as does the less strong overlap between the conifer-oak forests and the mixed chaparral samples. These overlaps indicate limits of resolution of the analog method when it is based on multivariate distance measures alone (cf. Calcote 1998).

Pollen representation and ratios as refinements of the analog method. In many cases of overlap, percentage representation of *Pinus* and *Quercus* pollen and ratios of these two pollen types can be used in addition to SCD relationships to determine a number of vegetation characteristics more precisely, and thereby greatly reduce the number of inappropriate analogies within the surface sample set. These capabilities include:

1) *Quercus* pollen $<\sim11.5\%$ indicates the local absence of oak trees in samples selecting both conifer-dominated and conifer-oak forest analogs, and *Quercus* pollen $>\sim18\%$ indicates the local presence of oaks in the same situation [sample 28 suggests that when relatively high levels of *Pinus* and Other Asteraceae pollen are combined in this situation, eliminating Other Asteraceae from the pollen sum might be useful to determine an oak percentage that is comparable to this criterion];

2) the ratio of conifer/*Quercus* pollen accurately reflects the relative coverage of conifers and oaks in samples selecting both conifer-dominated and conifer-oak forest analogs;

3) *Conifer* pollen $<\sim6.5\%$ distinguishes scrub and oak woodland vegetation from conifer-dominated and conifer-oak forests when SCD relationships across these vegetation groups indicate analogy (with the exception of stands devoid of pine within a conifer-oak forest matrix [sample 27]); and

4) the percentage of *Quercus* pollen is more than two times larger in oak woodland samples than in mixed chaparral samples, allowing inappropriate analogies between these vegetation types to be resolved.

In addition, ratios of other pollen types can resolve inappropriate analogies that do not involve *Pinus-Quercus* relationships. A ratio of *Pinus*/Cupressaceae-undifferentiated pollen $<\sim4.0$ successfully identifies the conifer-dominated forests with significant cover of western juniper from the rest of the conifer-dominated forests. This test cannot, however, distinguish forests with high representation of western juniper from conifer-oak forests with high representation of incense cedar (sample 24). In this case, the *Quercus* pollen representation test ($>\sim18\%$) can separate sample 24 from the high-montane samples. The ratio of *Pinus*/*Artemisia* pollen successfully distinguishes the conifer-dominated forests from sagebrush-pine steppe vegetation; this ratio is 2.4 for sample 35 (steppe) and always exceeds 6.3 for the conifer-dominated for-

ests. This use of pollen ratios to resolve ambiguities that arise when using dissimilarity metrics for analog selection in this data set parallels the results of Calcote (1998).

Use of Surface Samples as an Analog Set for Paleoecological Reconstruction

The SCD results reported here indicate that the analog method applied with this surface sample set is generally capable of distinguishing the important vegetation types in the montane and foothill regions of cismontane southern California—especially when extended by identification criteria based on specific pollen proportions and pollen ratios. Since the vegetation types in the region are associated with climate and elevation gradients, the ability of the extended analog method to distinguish the vegetation types suggests climate and apparent elevation reconstructions based on this method should be capable of good quality. Rigorous, quantitative tests of these conclusions are developed and examined in Wahl (2003).

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Appendix 1

Characteristics of Conifer Pollen Representation at Fossil Meadow Sites

Samples 18–20 near Taquitz Meadow in the San Jacinto Mountains (~60 m diameter, 2399 m elevation; Table 1, Fig. 1) form a transect from the meadow's edge (20) into the surrounding pine-dominated forest (19 and 18, respectively). (The pines in this forest are *Pinus jeffreyii* and *P. ponderosa*.) This transect is ~150 m long, going up a gentle SE-facing slope. The higher percentages of *Pinus* pollen (73% and 69%) in the samples further into the forest, in comparison to the meadow edge (59%), suggest that meadow sites may be expected to show diminished representation of conifer pollen in relation to smaller openings within surrounding forests. This suggestion is confirmed by the pollen spectra from samples in and near another fossil site, Hual Cu Cuish Meadow in the Cuyamaca Mountains (Table 1, Fig. 1). In this larger, lower meadow (~500 m × ~100 m, 1433 m elevation), a mid-meadow surface sample (31) has 20% conifer pollen (9% *Pinus,* 9% Cupressaceae-undifferentiated, and 2% *Abies*) and a second sample ~10 m from the forest edge (32) has 22% conifer pollen (11% *Pinus,* 10% Cupressaceae-undifferentiated, and 1% *Abies*).[†] Two nearby samples from smaller openings in the mixed conifer-oak forest surrounding the meadow have: a) 60% conifer pollen (37% Cupressaceae-undifferentiated, 20% *Pinus,* and 3% *Abies*) in part of the forest with tree-layer coverage of 30% incense cedar, 25% pines (*P. ponderosa, P. lambertiana,* and *P. jeffreyii*), 25% *Quercus kellogii* (black oak), and 20% white fir (sample 24); and b) 38% conifer pollen (nearly all *Pinus*) in a forest opening with 70% pines (*P. jeffreyii, P. ponderosa,* or possible hybrids of these two taxa) and 30% black oak in the tree layer (sample 28) (coverage data from Wahl 2002).

The data from Hual Cu Cuish Meadow indicate that relatively low levels of conifer pollen (~20% total and ~10% *Pinus*) can occur in larger meadows surrounded by forest in which pine and other conifers are important, even dominant canopy trees. This characteristic is consistent with the results of Anderson and Koehler (2003), who also report 10% as the lower threshold for *Pinus* pollen where pine trees are present, and with surface samples from mountainous areas in nearby northwestern Mexico, in which a *Pinus* pollen threshold of 10–15% is reported as indicative of adjacent forest with a significant proportion of pines (Orvis 1998). This characteristic of pollen representation in the montane forests of southern California and nearby Mexico contrasts strongly with the pollen spectra of surface samples in many parts of North America east of the Rocky Mountains; in the latter part of the continent, *Pinus* percentages below 20–25% most likely indicate "background" levels, and few or no pines in the nearby vegetation (cf. McAndrews and Wright 1969; Calcote 1998).

[†] These two samples were taken from the typical surface of this meadow (away from the coring site in a small cattail (*Typha*) marsh), which is currently less saturated than those of the other meadow fossil sites (Wahl 2002). Few wet-indicating plants were growing at these sample sites (Wahl 2002) and very little pollen from wet-indicating taxa occurred in their pollen assemblages (Fig. 2); thus these samples are not subject to biases caused by coverage of hydric, meadow-specific vegetation and are comparable to the other surface samples.

SEQUENTIALLY ADJUSTED SEX-RATIOS IN GYNOMONOECISM, AND *POA DIABOLI* (POACEAE), A NEW SPECIES FROM CALIFORNIA

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Abstract

Poa diaboli is described as a new and rare species of *P.* subsect. *Madropoa* from the coastal mountains of southern California. Its breeding system is like that in species of *Poa* previously said to be partially gynodioecious. However, in species of *Poa* with the corresponding breeding system syndrome, plants that are totally pistillate-flowered are rare and possibly only late-flowering individuals. We conclude that the breeding system of these species of *Poa* is better classified as a new subset of gynomonoecism, here termed sequentially adjusted gynomonoecism. Subtypes of gynomonoecism in the grasses, and in *Poa,* are outlined.

Key Words: breeding systems, Gramineae, grass, gynomonoecism, *Poa,* Taxonomy.

The new species of *Poa* L. was possibly first collected by David Keil in 1998. Because of its uncertain identity, and isolated geographical occurrence from similar species, it was brought to the attention of first author. It was initially thought to be dioecious, but further investigation of new collections with longer series of specimens, revealed that it is either weakly gynodioecious or exhibits an unusual form of gynomonoecism.

Poa (subsect. *Madropoa*) **diaboli** Soreng & Keil, sp. nov. (Fig. 1)—TYPE: USA, California, San Luis Obispo Co., W end of San Luis Range, Montana de Oro State Park, slopes W of Valencia Peak, very local on steep N facing slope in coastal scrub, 164–245 m, 27 March 1998, *D. Keil 26474* (holotype: US, isotypes: OBI-55333, [CAS, K, RSA; to be distributed])

A Poa confine *robustiore, altiore (26–50 cm versus 7–30 cm), paniculis longioribus (4–8.5 [10.5] versus 1–5 cm), diffusioribus, laminis planis vel plicatis, lemmatis longioribus ([3.2–] 4.25–5 versus 2.4–4 mm), venis sine pilis, rachillis visibilis longioribus plerumque asperate sine pilis, plantis gynomonoeciis, antheris plerumque longioribus ([1.4] 1.75–2.6 versus 1.5–2 mm), differt.*

Sequentially adjusted gynomonoecious, perennial grass, rhizomatous and stoloniferous, forming loose, leafy, tufts up to 25 cm tall and 30 cm across. Vegetative shoots numerous, shoot emergence extravaginal with rudimentary prophylls, and pseudo-intravaginal with tubular prophylls, and intravaginal with well developed prophylls. Culms 26–50 cm long, 0.5–0.9 mm diam., numerous, widely spreading to sortly decumbent and erect, leafy, one or more nodes exposed, uppermost node in lower third to middle of culm, frequently branching above the base with several shoots developing in from adjacent nodes with contracted internodes. Leaves; cataphylls present on extravaginal shoots; sheaths keeled, lightly scabrous, uppermost 4.5–9 cm long, margins fused ⅖–⁷⁄₁₀ the length; collars scabrous to pubescent on margins; ligules of middle and upper culm leaves 1.0–3.0 mm long (of lateral shoots and basal culm leaves less than 1 mm long), apex truncate and lacerate to (mostly) obtuse or acute, apically scabrous, abaxial surface moderately to densely scabrous; blades flat (especially upper culm ones) or more often folded, thin, slender, 0.8–2.0 (–2.5) mm wide, narrowly prow-tipped, abaxial surface smooth, veins prominent, keel and margins scabrous, adaxial surface of innovation blades sparsely to moderately densely scabrous or short-hairy on and between the veins (infrequently glabrous between veins), culm blades generally gradually decreasing in length upwards, uppermost blades 2.9–6 (–7) (pistillate specimens), or (3–) 4–8.6 (–11) (perfect specimens) cm long; upper-sheath to blade-length ratio 1.4–2.4: 1, averaging 1.8 (pistillate specimens), 0.6–2.1: 1, averaging 1.4 (perfect specimens). Paniculate synflorescences exerted above the vegetative mounds, erect to nodding, pyramidal to ovate, open, or eventually loosely contracted, sparse, 4.0–8.5 (–10.5) cm long; branches 1–2 per node, spreading to ascending, slender, moderately strict, angled, moderately to densely scabrous mainly along angles, with spikelets in the distal ½, longest branches 2.1–4.5 (–7) cm. Spikelets lanceolate, 5.3–9 mm long; glumes
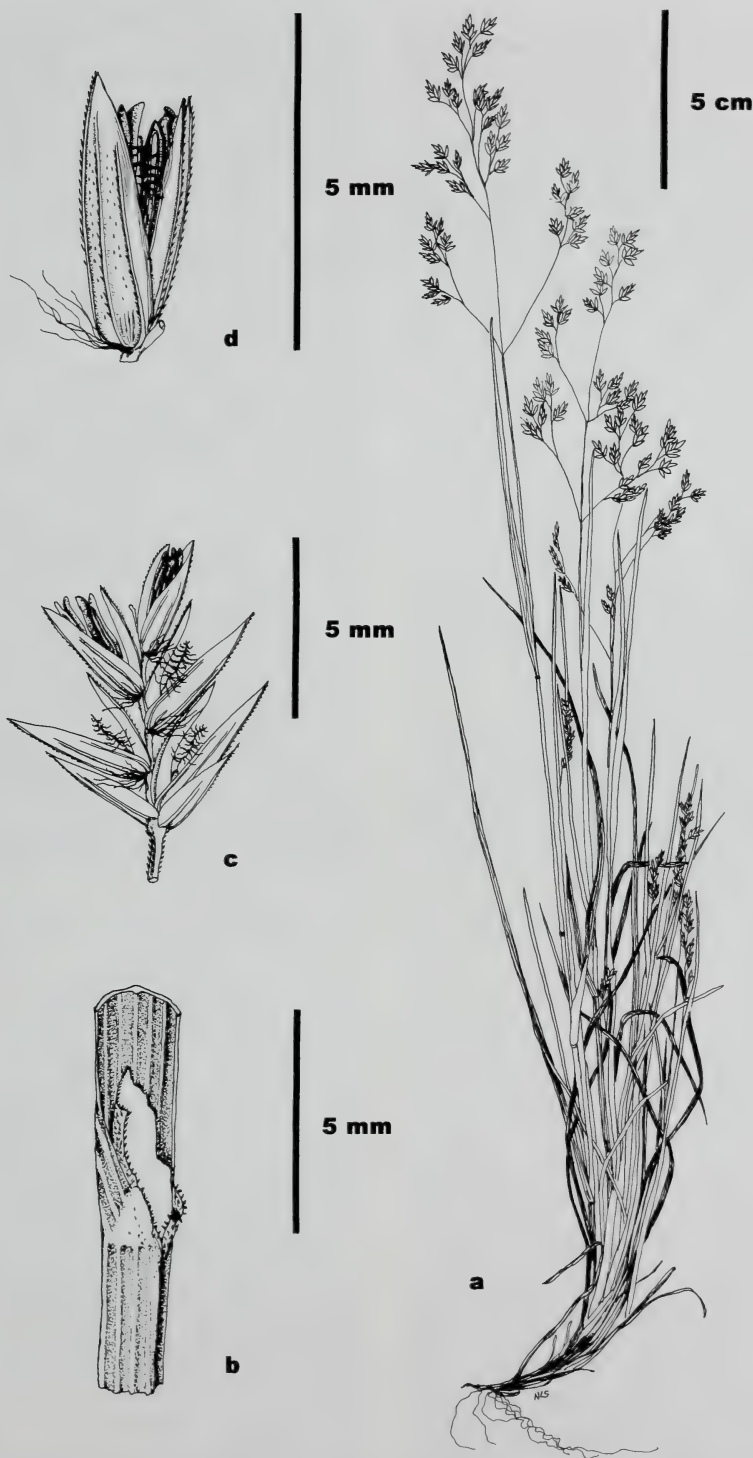
Fig. 1. *Poa diaboli.* Illustration of *Keil 26474,* holotype US; a) habit; b) ligule; c) spikelet (perfect-flowered); d) floret.

narrowly lanceolate, 3-veined, lower (2.0–) 2.7–3.8 mm long, upper, (2.3–) 2.9–3.9 mm long; rachilla internodes 1.0–1.3 mm long, laterally visible, sparsely to densely, coarsely scabrous or infrequently entirely smooth; florets (2–) 3–6 (–7); calluses webbed, webs diffuse, arising around the lemma base, hairs thin, sinuous reaching as far as mid-lemma, sparser and shorter laterally, or loosely concentrated dorsally and absent laterally; lemmas pale green throughout, to anthocyanic along the margins to apex or throughout, lanceolate to narrowly lanceolate, (3.2–) 4.25–5.0 mm long, fairly thin, strongly keeled, apex acute to narrowly acute (infrequently the keel vein excurrent as a tiny mucro), margins very narrowly hyaline, surface sparsely to moderately-densely scabrous throughout, glabrous, veins 5, prominent, moderately to densely scabrous, lateral veins extending to within 1 mm of upper margins; paleas ⅚ to = lemmas in length, keels coarsely and closely scabrous, surface between keels narrow, scabrous. Flowers bisexual or pistillate; anthers (1.4–) 1.75–2.6 mm long, or rudimentary and sterile; ovary glabrous, fully matured caryopses unknown; lodicules 1.0 mm long, broadly lanceolate, long lobed. Chromosome number unknown.

Flowering. March to April.

Habitat. North facing slopes and ridgetops within 2–3 km of the Pacific coast, fire successional area of mesic chaparral, grassy coastal-scrub, coastal live oak woodland, and mesic Bishop pine forest, thin soils over an Edna Shale substrate, 120–400 m elev.

Distribution. United States, California, San Luis Obispo Co., San Luis Range (also known as the Irish Hills).

Paratypes. USA. California, San Luis Obispo Co., NW end of San Luis Range: Montana de Oro State Park, slopes W of Valencia Pk., ca. 230 m, 27 Apr 1998, *D. Keil 26941* (OBI); N slopes of Valencia Pk., 35°15′50–54″N × 120°52′19–24″W, 240 m to 383 m, 7 Apr 2003, *R. Soreng, E. Frenzel, S. Krenn & J. Blecha 7401* (US); Pacific Gas & Electric, Diablo Canyon power plant lands, North Ranch, 0.4 km E from coast road on Crowbar Canyon Rd., 35.228°N × 120.8640°W, ca. 120 m, 19 Apr 2001, *D. Keil & E. Frenzel 29331* (OBI); same loc., 120 m, 6 May 2001, *E. Frenzel & D. Haines s.n.* (OBI; DNA voucher); North Ranch, ridge above Coon Cr. Canyon, 35.243°N × 120.876°W, ca. 365 m, 19 Apr 2001, *D. Keil & E. Frenzel 29336* (OBI); 0.3 km inland from coastal road along Crowbar Canyon Rd. at mouth of Crowbar Canyon, ca. 120 m, 14 Apr 2001, *E. Frenzel DC-19* (OBI); Ridge top S of Coon Cr., ca. 0.5 km E of "Last" benchmark and above road cut, ca. 400 m, 27 Mar 2001, *E. Frenzel & D. Haines 81* (OBI).

Conservation status. Narrowly endemic, locally frequent. The geographic range known from collections may be less than 15 sq km. However, it occurs in very rugged country, and estimates of potential habitat suggest the range is somewhat larger. It was reportedly collected from the San Luis Range in Ruda Canyon (*Glenn Clifton* in 1993), but we have not been sucessful in locating the voucher.

Presumably the species was overlooked because until recently the surrounding lands were mostly in large private holdings and extensively grazed. Light grazing of continues on some of the Diablo Canyon Power Plant land. Montana de Oro State Park (MOSP) land was privately owned until the late 1960's and was grazed until the early 1970's. The coastal bench lands were used for military exercises for a short period prior to the establishment of the state park (Sally Krenn, Jim Blecha personal communication). Attempts to revegitate MOSP lands, and eradicate the invasive *Ehrharta calycina* (Velt Grass), included a controlled burn covering the area from the coastal bench to the top of Valencia Peak in 1997 (Vince Cicero personal communication). David Keil first noticed the new species in an area of recently burned chaparral vegetation in the following year. The largest population of the new *Poa* yet discovered occurs on the peak area, and it seems the fire did not adversely impact this population, and may have benefited it.

The new species epithet, *diaboli* (spelling verified in Kunkel 1990), commemorates both its occurrence on grounds of the Diablo Canyon Nuclear Power Plant, and secondly the difficulties it has caused the authors in determining its affinities and its breeding system.

BREEDING SYSTEM DETERMINATION

Dicliny is widespread in the Poaceae (R.Br.) Barnh. (Connor 1979). However, gynomonoecism is considered uncommon, occurring in only eight genera and not in all species of those (Connor 1979). Connor characterized several variations in the pattern of sex expression among genera of gynomonoecious grasses, and all cases seem to be more or less spatially fixed in expression, and sequentially regular. Pistillate flowers consistently occur in a specific orientation, either within spikelets, or within pairs or sets of spikelets (Connor 1979), and, although there may be differces in timing of flowering, there are no reported changes in the ratio of one type of flower to another through the growing season in gynomonoecious species. The variations may be categorized as follows:

I. Spikelets all alike, certain florets consistently pistillate.
   a) proximal floret pistillate, distal floret(s) perfect.
   b) proximal floret(s) perfect, distal floret(s) pistillate.
II. Spikelets pistillate or perfect, these arranged in pairs or sets.

a) sessile spikelet perfect, pedicellate spike-
let pistillate.

b) sessile spikelet pistillate, pedicellate
spikelet perfect.

c) lateral spikelets pistillate, terminal spikelet
perfect.

Most of Connor's reports of gynomonoecism
come from species or genera belonging to grass
tribes or subfamilies in which the number of florets
per spikelet is fixed at either one or two (subfam.
Ehrhartoideae Link trib. Olyreae Kunth ex Spenn.,
subfam. Panicoideae Link, respectively), and where
paired spikelets are common. Connor (1979) re-
ports gynomonoecism in species with spikelets with
indeterminate numbers of florets only from *Cento-
theca* Desv. (subfam. Panicoideae trib. Centothe-
ceae Ridl.), *Munroa* Torrey (subfam. Chloridoideae
Kunth. ex Beilschm.), and *Poa* (subfam. Pooideae
Benth.). In each of these genera the syndrome is
different. *Munroa* fits categories Ia and IIc (above),
and *Centotheca* and *Poa* fit category Ib. In *Cento-
theca* only the proximal floret is perfect and those
distal to it are pistillate. In *Poa,* generally only the
distal most floret is pistillate, and all more proximal
florets are perfect. We are not aware of any reports
of changes in the frequency of pistillate flowers
through time in gynomonoecious grasses.

The breeding system of *Poa diaboli* falls on the
borderline between gynomonoecism and gynodioe-
cism. To characterize the breeding system of the
new species, individual specimens (pre-2003) were
checked for presence or absence of perfect or pis-
tillate flowers (i.e., those with developed pistils and
rudimentary anthers; there seem to be no staminate
flowers). For this analysis individual specimens
were considered to be samples with one or more
synflorescences attached to a shared base, or single
flowering shoots that were pressed or mounted on
the same sheet and appear to be from the same
individual: The individual specimens do not nec-
essarily represent different plants, and more precise
study of individuals through a season and through
successive years is needed in the future. We assume
that male sterility, as indicated by the occurrence
of rudimentary anthers, is under genetic control,
that anthers are not simply aborted due to environ-
mental factors (i.e., disease, moisture or nutrient
stress, temperature shock, etc.; though possibly
triggered by these), nor due to genetic abnormali-
ties. The occurrence of rudimentary anthers is reg-
ular enough within and among specimens that this
seems to be a warranted assumption. Moreover, the
pattern is consistent with that found in other species
of diclinous *Poa* (Soreng 1991, 2000). In geneti-
cally imbalanced plants of *Poa,* if anther abortion
occurs, it usually occurs in a late stage of devel-
opment, and some pollen is formed, although usu-
ally malformed to some degree (RJS personal ob-
servation). However, in diclinous species, as in the

present case, anther development is halted at a
much earlier, presumably pre-tapetal, stage.

There are three completely pistillate specimens
among an estimated 20 specimens with at least
some perfect-flowers. These three specimens may
represent truly pistillate plants, or late flowering
plants that, had they developed earlier, would also
have produced shoots with perfect-flowers, or
plants in which pistillate shoots have become sep-
arated from shoots with perfect-flowers in the pro-
cess of collecting the plant. In seven of the speci-
mens with perfect-flowers there are some panicles
with a few pistillate spikelets among the lower
spikelets of their synflorescences, and three speci-
mens with early maturing mainly or wholly perfect-
flowered panicles and late maturing, smaller, com-
pletely pistillate-flowered panicles.

In a survey of the Valencia Peak population in
2003 (*Soreng et al. 7401*) one synflorescence was
taken off of 42 plants at least 2 m apart. The syn-
florescence count was; three pistillate-flowered, five
partly perfect-flowered/partly pistillate-flowered,
and 34 perfect-flowered. Both the pre-2003 speci-
men count and the 2003 population census results
suggest that the new species is either intermediate
between being gynomonoecious and gynodioe-
cious, or, more likely, as no completly pistillate
plants were found, the ratio of pistillate and perfect
flowers is sequentially adjusted.

A corresponding syndrome is present in a several
other species of *Poa.* This includes co-occurrence
within populations of: 1) many individuals that are
perfect-flowered only, along with a high percentage
of individuals (but averaging less than half) that
have mixtures of perfect and pistillate flowers; 2)
within mixed-flowered individuals, pistillate flow-
ers occur in terminal florets within some spikelets,
and often in all flowers of spikelets below the
mixed-flowered spikelets, both arrangements in-
creasing in frequency in late developing (lower)
parts of synflorescences, and in later developing
synflorescences; 3) some late developing, com-
pletely pistillate synflorescences, in individuals
with earlier developing perfect-flowered, or partly
perfect-flowered synflorescences; and, 4) few (or
no) individuals having only pistillate flowers, but
then all synflorescences developing late in the
breeding season. This syndrome is characteristic of
the *Poa* sect. *Homalopoa* Dumort. "*P. nervosa*
complex" of North America (i.e., *P. arnowiae* So-
reng, *P. cuspidata* Nutt., *P. nervosa* (Hook.) Vasey
s.str., and *P. tracyi* Vasey; three other species in
this complex are dioecious (*P. sierrae* T.J. Howell),
subdioecious (*P. rhizomata* Hitchc.), or dioecious
and gynodioecious (*P. chambersii* Soreng); see So-
reng and Hatch 1983; Soreng 1991, 1998, 2000).
The same syndrome has also been diagnosed in
populations studied in the field and lab in a few
South American species (e.g., *P. fibrifera* Pilg., an
undescribed species from southern Peru and north-
ern Chile, *Peterson & Soreng 15615* [CONC, US]),

and a few southeast Asian species (e.g., *P. grandis* Hand.-Maz., *Soreng, Peterson & Sun 5628*; [KUN, PE, US] RJS personal observation).

This breeding system, which seems more like gynomonoecism, differs from true gynodioecism wherein pistillate individuals are clearly distinct, occur in a more regular and higher proportion to perfect-flowered individuals (but not much more than half), and also mature more or less simultaneously with those (at least in *Poa*; RJS personal observation). Soreng and Hatch (1983), and Soreng (1991, 2000), previously identified this syndrome as "partial gynodioecy". However, because, in the several species with this syndrome, individual plants that are totally pistillate throughout a season are rare or uncommon, RJS is inclined to agree with David G. Lloyd (personal communication 1992) that the syndrome is more like an extreme, and previously unrecorded, form of gynomonoecism, than like weak gynodioecism. This form of gynomonoecism is not easily distinguished from gynodioecism without careful examination of the distribution of different-sexed flowers in multiple populations in the field and common-garden studies, however, few totally pistillate plants are expected, along with a shift to pistillate flowers as the season progresses (Lloyd 1974, 1980).

There seems to be a need to differentiate subtypes of gynomonoecism in *Poa*, so we shall call this system "sequentially adjusted gynomonoecism" to distinguish it from the common form of gynomonoecism in other *Poa*, and seemingly in other grasses, in which sex expression is fixed in spatial orientation, and is not known to change in frequency through time. Outside Poaceae, Acevado-Rodríguez [2003] identified a syndrome in *Talisia* (Sapindaceae) in which individuals are "sequentially monoecious", shifting from staminate to pistillate flower production and back to staminate flowers within a season. We are unaware of any reports of sequentially adjusted sex expression in gynmonoecious plants. Here we take up the terms "sequentially adjusted" to denote the temporal shift in sex expression through the growing season. In other gynomonoecious *Poa*, sex expression is fixed in frequency and time. In *P. annua* L. and other species of *P.* sect. *Ochlopoa* Asch. & Graebn., and many South and Central American species, and some Himalayan species, pistillate flowers are consistently and only produced in the terminal floret, or less often also in the subterminal floret, within spikelets (Hackel 1904; Nannfeldt 1938; Chrtek and Jirásek 1962; Connor 1979; Anton and Connor 1995). The latter syndrome is common, and may be distinguished as fixed-sex-expression gynomonoecism. These species are not known to produce any pistillate spikelets, mostly pistillate synflorescences, or any totally, perfect-flowered individuals. Moreover, there is no known change in frequency of pistillate florets through time, within or between plants.

In their paper on "Floral biology and reproduction in *Poa*" Anton and Connor (1995) described the many variations in *Poa* breeding systems known to them. They noted Soreng's application of the term "partially gynodioecious" to several North American species, but indicated their unfamiliarity with this variation, also suggesting that it might represent an exaggerated form of gynomonoecism. They comment on the uniformity of the syndrome of gynomonoecism in many South and Central American species of *Poa*, and in species of the European (now cosmopolitan) *P.* sect. *Ochlopoa*. In these species, the lowermost 1 or 2 florets of 2 or 3 (–4) flowered spikelets are perfect, and the upper floret is pistillate. This also occurs in several Himalayan species of *Poa* (e.g., *P. sikkimensis* (Stapf) Bor; RJS personal observation from herbarium specimens and *Soreng, Peterson, & Sun 5676* [KUN, PE, US]). Seed is normally set in both types of flowers. They report no evidence of variation in flowering among most gynomonoecious *Poa* (except for *P. supina* Schrad. of Europe, in which the pistillate florets open one day before the perfect ones within the same spikelets). They indicate that in a few gynomonoecious species all flowers may be pistillate or perfect in some plants or synflorescences (e.g., *P. glomerifera* Hack., *P. horridula* Pilg.). The latter two species, like *P. fiberifera, P. grandis,* and others mentioned above, may also exhibit sequentially adjusted gynomonoecism (RJS personal observation from study of herbarium specimens; also observed by Maria Negritto personal communication).

RELATIONSHIPS AND IDENTIFICATION OF THE NEW SPECIES

Although *P. diaboli* seems to share sequentially adjusted gynomonoecism with species of *P.* sect. *Homalopoa* s.lat., the North American species of that group occur in forested habitats, and have much broader leaves and more loosely-tufted, erect habits, and lack hairs on the adaxial surface of innovation blades. Also, if those have a web on the callus, as most species of *P.* sect. *Homalopoa* and other *Poa* do, they have a single, tight, dorsal tuft of hairs. If the new species were gynodioecious, this would support a close relationship to species of *Poa* sect. *Madropoa* Soreng, especially those of the rhizomatous subsection *Madropoa* Soreng. If it exhibits sequentially adjusted gynomonoecism, as we think, this species might represent an early transitional element between the *P. nervosa* complex and *P.* sect. *Madropoa.*

In comparison with species of *P.* sect. *Madropoa, P. diaboli* is unusual in the possession, in some specimens, of thin, flat culm leaves, and folded leaves that lack long, hooked or sinuous prickle hairs on and between the veins of upper leaf-blade surfaces, even on innovation shoots. In these features, it approaches *P. leibergii* Scribn. (of mossy,

shaded cliffs and open slopes where snow pockets remain into early spring, of the Columbia Plateaus; gynodioecious) and *P. stebbinsii* Soreng (of subalpine wet meadows, of the high Sierra Nevada; gynodioecious), both of *P.* sect. *Madropoa* subsect. *Epiles* Soreng. However, *P. diaboli* more often does have hairs on and between the veins of adaxial blades surfaces of its innovation shoots, like most other *Madropoa* species. Moreover, it has the additional features of a rhizomatous and/or stoloniferous habit, and a diffusely cobwebby callus, typical of species *P.* sect. *Madropoa* subsect. *Madropoa* Soreng

The hairs of the callus in *Poa diaboli* are long, soft, and sinuous, as in most *Poa,* but are more or less, diffusely distributed around the sides and back of the callus in many florets. The form and insertion of the callus hairs most closely resemble those found in *P. confinis* Vasey (of coastal dunes and adjacent sandy forests, from southernmost Alaska south to Pt. Reyes in Marin Co., California; gynodioecious to dioecious), *P. douglasii* Nees (coastal dunes, from Mendocino Co. south to Pt. Sur, Monterey Co., with isolated populations at Vandenberg Air Force Base, south base [a new record, *D. Keil 24742*], and on San Miguel and Santa Rosa Islands of Santa Barbara Co.; dioecious), and *P. piperi* Hitchc. (of forest openings on serpentine, endemic to the Klamath–Siskiyou region of southwest Oregon and northwest California; dioecious), all of *P.* subsect. *Madropoa. Poa confinis* is gynodioecious to dioecious (n = 90, sex ratio 1.4:1, pistillate-flowered individuals to staminate-flowered, perfect-flowered, and mixed perfect and pistillate-flowered individuals).

In our estimation, despite some differences in morphology and breeding system, *Poa diaboli* belongs to *P.* subsect. *Madropoa* where it approaches *P. piperi,* but is most similar to *P. confinis*. In most characteristics examined the new species is larger than *P. confinis,* but range of variation measurements often overlap. However, among other differences noted above, the lemmas of *P. confinis* are usually at least sparsely short hairy on the keel, whereas the new species is devoid of hairs (other than fine hooks or prickle hairs) on the lemma. In the treatment of *Poa* (Soreng 1994) in *The Jepson Manual: Higher Plants of California* the new species keys out to a choice between *P. kelloggii* and *P. piperi*. Different specimens key to one or the other but fit neither species description. Lead number nine may be modified as follows:

9a.   Sheaths of upper culm leaves open most of their length; innovation blades smooth or mainly scabrous over the veins adaxially; synflorescences 10–20 cm long; flowers all perfect . . *Poa kelloggii*
9a′. Sheaths of upper culm leaves closed over ⅓ of their length or more; innovation blades often hairy adaxially; synflorescences 4–10 cm long; flowers all perfect or some unisexual.
9b.   Leaves thin, soft, mostly 0.8–1.5 mm wide and

folded, or up to 2.5 mm wide and flat, those of the culm gradually reduced in length upward, frequently flat; lemmas up to 5 mm long; plants perfect-flowered or some (rarely all) flowers pistillate . . . . *Poa diaboli*
9b′. Leaves thicker, somewhat firmer, mostly 1.5–3 mm wide, those of the culm sharply reduced in length upward, never flat; lemmas mostly 5–7 mm long; plants nearly all pistillate or staminate-flowered . . . . *Poa piperi*

The morphology and transitional breeding system suggest *Poa diaboli* is either a geologically old element in *P.* subsect. *Madropoa,* or that it is an isolated population, likely derived from *P. confinis,* or its progenitor, which has reverted to a more perfect-flowered breeding system in the face of density dependent pollination factors.

Few native species of *Poa* are known from the San Luis Range or the adjacent and more inland Santa Lucia Range (*P. howellii* Vasey & Scribn., *P. secunda* J. Presl subsp. *secunda* [*P. scabrella* (Thurb.) Vasey form]). The new species is readily distinguished from *P. howellii,* which occurs in the Santa Lucia Range, and in Price Canyon in the San Luis Range, by its strongly perennial habit, absence of soft hairs on the body of the lemma, diffuse callus web, and its longer anthers. From *P. secunda s.lat.,* common and widespread western North America, and sympatric with the new species (DJK personal observation; also recorded from the south end of the San Luis Range, *Dudley s.n.,* SU), it is distinguished by the rhizomatous habit, presence of strongly keeled lemmas with a narrowly hyaline margin, more closed culm sheaths, and presence of a well developed web on the callus, and from *P. secunda* subsp. *secunda* (the only subspecies in the region) by the lack of any soft or crisp hairs on the lemma surface.

Chloroplast DNA (cpDNA) restriction site data (Lynn Gillespie personal communication) has confirmed the postulated relationship of *P. diaboli* with members of a clade including species of *P.* sects. *Homalopoa* and *Madropoa,* and refuted membership in many other sections including *P.* sect. *Sylvestres* Soreng (including *P. kelloggii,* and *P. marcida* Hitchc., also new cpDNA data) and *P.* sect. *Secundae* Soreng (including *P. secunda*) (see Soreng 1990, for a general cpDNA phylogenetic hypothesis for *Poa*).

Of introduced species reported from San Luis Obispo Co., only the annuals *Poa annua* L., and *P. infirma* Kunth (RJS personal observation 2003), are known to occur in the area, but these have little in common with the new species.

It is reasonable to postulate that the isolated geographic occurrence of *Poa diaboli* in the south central California coastal hills represents a relictual Pleistocene distribution for species of *P.* sect. *Madropoa,* as the nearest station for its closest relative, *P. confinis,* is over 325 km to the north. Other sec-

tional members (other than *P. douglasii*) are dis-
tributed much further north or well inland.

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SELF-INCOMPATIBILITY AND POLLEN LIMITATION TO SEED SET IN
DITHYREA MARITIMA (BRASSICACEAE)

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Knowledge of the breeding and pollination systems of rare plants is essential for their effective management (Sipes and Tepedino 1995; Kearns and Inouye 1997; Kearns et al. 1998). Pollinators may affect the viability of rare plant populations by regulating fecundity, inbreeding, and the ability to adapt to environmental change. The nature of this effect will depend on an interaction between the behavior of pollinators and the breeding system of the plant (Aigner in press). For example, if plants require pollinator visits to effect seed set, then the frequency of visits and the efficiency with which pollen is transferred on each visit will have direct effects on plant fecundity. If seed set is not pollen limited, pollinators may have more subtle effects on the viability of plant populations. If genetic variation within plant populations is spatially structured, then the interplant distances moved by pollinators will determine the level of inbreeding and potentially the fitness of offspring (Ellstrand and Elam 1993). Even if plants are predominantly selfing, a loss of pollinators may reduce rates of genetic recombination and the ability to evolve defenses against herbivores or parasites (Lively 1996). In all of these cases, conservation of rare plants also requires management of the pollination process.

Here, I describe the breeding system and pollination of *Dithyrea maritima* Davidson (beach spectacle pod), a rare perennial herb endemic to coastal sand dunes in Southern and Baja California. *Dithyrea maritima* historically occurred from San Luis Obispo to Los Angeles County, with a disjunct population at El Socorro, Baja California (Rollins 1979). It is now listed as a threatened species by the State of California, where it currently persists only at Morro Bay, the Guadalupe-Nipomo Dunes, Vandenberg Air Force Base, and on two of California's Channel Islands—San Miguel and San Nicolas. No formal monitoring of *D. maritima* population trends has occurred, but surveys and casual observations within its remaining range suggest that populations are either stable or declining (Rollins 1979; Junak et al. 1995; Aigner and Waser 2001).

Dithyrea maritima reproduces rhizomatously and by seed. Individual ramets consist of a rosette of fleshy leaves usually less than 2 dm tall or wide. Between April and July, racemes of densely clustered, fragrant, white-to-cream colored flowers (sometimes tinged with purple) are produced. Each flower may produce an indehiscent, spectacle-like fruit (silique), bearing one or two seeds. I studied *D. maritima* at four sites encompassing most of its range in Southern California: San Miguel Island, San Nicolas Island, Vandenberg Air Force Base (VAFB), and the Guadalupe-Nipomo Dunes.

Two partly overlapping experiments were used in 1998 to describe the breeding system of *D. maritima*. In the first (Experiment 1), I used an intensive set of treatments at VAFB to determine the extent of self-compatibility and the importance of animal visitation to seed production. In the second (Experiment 2), I used a skeleton set of treatments at all four sites to investigate whether the breeding system and importance of animal visitation varies among sites.

Experiment 1 was a randomized complete block design in which each block consisted of four ramets of similar size and vigor (within an approximately 1.5-m radius) chosen from a naturally delineated patch of ramets which was itself located 50 to 300 m from the nearest adjacent block. Treatments consisted of (1) testing for autonomous self-fertilization by covering plants with cages to exclude pollinators, (2) testing for self-compatibility by covering plants and adding pollen from the same plant, (3) testing for the importance of outcrossing by covering plants and adding pollen from a different genet, and (4) leaving plants unmanipulated to allow normal visitation. Experiment 2 used treatments 1 and 4 applied at all four sites.

Cages for excluding pollinators were constructed from nylon bridal veil stretched over cylindrical wire frames that were large enough to prevent contact between mesh and plant. At each site I deliberately selected the location of the blocks to encompass the range of habitat variation; VAFB had five blocks and each of the other sites had eight.

The experimental unit was a single flowering ramet. In Experiment 1 I applied hand pollination treatments to all flowers on each ramet every one to six days between 5 May and 11 June, so that most flowers produced by a ramet were pollinated at least once during their lifetime (ca. 5 d).

The percentage of flowers setting fruit (producing either one or two seeds) was used as a response variable. This is because after fruits dropped from

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TABLE 1. MEAN PERCENT OF FLOWERS SETTING FRUIT (±ASD) IN A 1998 EXPERIMENTAL MANIPULATION OF POLLINATION SERVICE TO *DITHYREA MARITIMA* AT FOUR SITES IN SOUTHERN CALIFORNIA. Dashes indicate that the specified combination of treatment and site did not occur.

Site	n	Autogamy	Selfing with vector	Manual outcross	Open pollinated
Vandenberg AFB	5	0.43 ± 0.96	0.29 ± 0.64	53.39 ± 19.27	0.36 ± 0.80
Guadalupe Dunes	8	0.00 ± 0.00	—	—	0.69 ± 1.35
San Nicolas Island	8	3.24 ± 9.17	—	—	2.08 ± 4.61
San Miguel Island	8	0.05 ± 0.13	—	—	0.19 ± 0.54

the plant it was difficult to determine whether one or two seeds had been produced, but it was always easy to distinguish flowers that had produced a fruit from those that aborted completely.

I measured the activity of potential pollinators of *D. maritima* at the two mainland sites by making 1-hr observations of haphazardly-chosen patches of ramets. Patches were usually naturally delineated subpopulations and contained from 10 to 325 open flowers. For each observation I tallied the total number of visits by animal species, the total number of open flowers, and computed a per-flower visitation rate. I conducted 12 observations at VAFB and 10 at the Guadalupe-Nipomo Dunes between 6 May and 12 June. Most observations occurred in daylight, although at least one observation at each site extended after sunset. At VAFB, I spent one entire night checking hourly for nocturnal visitors. Pollinator observations for the two island sites are reported elsewhere (Aigner in press).

Experiment 1 indicated that *D. maritima* is largely self-incompatible; fruit set was negligible for all treatment groups except the hand outcross, in which fruit set was 53.4% (Kruskal-Wallis P = 0.003, Table 1). Fruit set in the hand outcross group probably would have been higher, except that many inflorescences were damaged by weevils and aphids before fruits could develop. Herbivory affected fruit set mostly at Vandenberg, where at least 50% of all inflorescences were damaged by herbivores (personal observation). Herbivory at the other 3 sites was rare.

I found no evidence from Experiment 2 that the degree of self-incompatibility varied across the geographic range of *D. maritima*. Fruit set for the autonomous self-fertilization group was <1% at all sites except San Nicolas Island, where it was 3.2% (Table 1). The higher fruit set on San Nicolas Island was entirely due to a single plant with 26% fruit set, and the difference among sites was not statistically significant (Kruskal-Wallis P = 0.69). The caged plant with 26% fruit set may have represented a breakdown of the self-incompatibility mechanism or may have resulted from the transfer of outcross pollen by insects such as beetles and ants that were not completely excluded by the cages.

Natural pollination service to *D. maritima* was poor at all sites. Fruit set among uncaged (open pollinated) plants was <1% at all sites except San Nicolas Island, where it was 2.08% (Table 1). This difference among sites was not statistically significant (Kruskal-Wallis P = 0.64). The percentage of flowers setting fruit also did not differ between uncaged and caged (autonomous self-fertilization treatment) plants (Kruskal-Wallis P = 0.18). Presumably most of the observed fruit set in the autonomous self-fertilization treatment group was due to pollination by small insects that were able to burrow under the cages. Throughout the study, and at all sites, I did observe minute beetles (at least some in the family Melyridae) and occasional ants within *D. maritima* flowers on both caged and uncaged plants. The beetles were usually head-down, inside the flower, at the base of the corolla and were typically covered in pollen. The stigma of *D. maritima* is large and capitate, and occupies almost the entire width of the corolla tube. If the beetles did travel between genets, they would probably transfer pollen as they squeezed past the stigma to reach the nectaries. The beetles were abundant and ubiquitous, so the lack of overall fruit set suggests that they infrequently moved between genets. Indeed, I never observed the beetles to move between flowers during observations of flower visitation, and consequently these beetles were not counted in estimates of pollinator visitation rates.

Consistent with the low fruit production seen in open-pollinated flowers, animal visitation to flowers of *D. maritima* was extremely rare at the two mainland sites. Flowers received an average of 0.022 (± 0.058 SD) visits/flower/hr and 0.006 (± 0.015 SD) visits/flower/hr at VAFB and Guadalupe-Nipomo Dunes, respectively. No visits occurred during the nighttime survey at VAFB, although moths were active in the area. Only 13 flower visits were observed in total. These were made by a variety of insects (flies, ants, bumblebees, and crickets), but rarely did I observe the same species visiting *D. maritima* more than once, and I never observed a particular visitor making sequential visits to flowers on different ramets.

Few pollinators were observed in this study, but pollination of *D. maritima* by bees does sometimes occur on San Nicolas Island, and bee visitation is associated with increased fruit set (Aigner in press). One season may have been insufficient to sample the spectrum of *D. maritima* pollinators on the

mainland. Indeed, some floral features (white flowers, a narrow corolla tube, and scent that seems to become stronger at night) of *D. maritima* suggest adaptation to moth pollination. Visitation by moths was not observed in this study and was rarely observed on San Nicolas Island (Aigner in press), but moth populations may be variable from year to year (Pettersson 1991) or even irruptive (Grant 1937).

Populations of *D. maritima* at all sites in this study were patchy, with discrete subpopulations of <10 to >1000 ramets separated by tens to hundreds of meters from adjacent subpopulations. Local subpopulations may persist even without seed production if their growth depends primarily on asexual reproduction; but because asexual reproduction occurs only by short-distance rhizomatous growth, formation of new subpopulations necessarily depends on production and dispersal of seeds. A set of surveys in 1992 and 1998–2000 on San Nicolas Island revealed high turnover of local subpopulations, with at least 5 subpopulations going extinct, 5 subpopulations newly colonizing, and only 2 subpopulations persisting over the 8 years (Aigner and Waser 2001). The apparent balance between extinction and colonization suggests that observed levels of seed production might be adequate to ensure overall population persistence, at least on San Nicolas Island. This possibility requires further investigation, because surveys were conducted by different observers and lacked consistent methods for recording the size and locations of subpopulations.

Ultimately, assessing the overall viability of *D. maritima* populations requires long-term studies of demography both at the subpopulation and metapopulation level (Schemske et al. 1994). Of course, estimating all relevant demographic parameters at two spatial scales is a substantial undertaking, particularly for a long-lived, clonally reproducing plant. Given limited resources for management, I suggest a more focused research strategy as a priority for conservation of *D. maritima*. First, to assess the status of *D. maritima*, i.e., whether populations are stable or declining, long-term monitoring of marked individuals within subpopulations and of the extinction and colonization of subpopulations should begin. A concurrent seed addition experiment within both occupied and unoccupied habitat patches would help resolve the importance of sexual reproduction to population persistence at both spatial scales. Given strong pollen limitation to seed set observed in this study and the potential to dramatically increase seed production by relatively simple manipulations (Aigner in press), augmentation of pollination and seed production seem like promising management tools if increased seed production can be shown to increase population

growth rates within patches or occupancy of potential habitat patches.

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A NEW COMBINATION IN *ATRIPLEX ARGENTEA* (CHENOPODIACEAE)

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Atriplex (Chenopodiaceae) is a genus of about 250 species of herbs and shrubs, 62 of which occur in North America north of Mexico. It occurs mainly in subarctic, temperate, and subtropical regions. In the process of preparing the treatment of *Atriplex* for Flora of North America, it became apparent that the combination *Atriplex argentea* Nuttall var. *mohavensis,* one of three varieties of *Atriplex argentea* recognized in *The Jepson Manual* (Taylor and Wilken 1993) and one of five varieties to be recognized in Flora of North America (Welsh in press), had never been validly published. To correct this, the combination is being made here.

Atriplex argentea Nuttall, Gen. N. Amer. Pl. 1: 198. 1818 * Silver orach

KEY TO VARIETIES

1. Plants low, rounded, mainly 1–3(–4.5) dm; fruiting bracteoles sessile or rarely some short stipitate, the appendages mainly acuminate or acute-attenuate; Nevada and adjacent se California, se Oregon.
2. Leaf blades typically, but not always, constricted to the petiole; herbage merely scurfy, or with elongate trichomes mainly on the fruiting bracteoles; Nevada (except the southern part), and adjacent se California and se Oregon . . . . *Atriplex argentea* var. *hillmanii* M.E. Jones
2. Leaf blades typically, if not always, cuneate to a winged petiole or merely sessile base; herbage copiously covered with elongate trichomes throughout, or mostly on the stems and fruiting bracteoles; Nye County, Nevada and adjacent Inyo County, California . . . . . *Atriplex argentea* var. *longitrichoma* (Stutz, Chu & Sanderson) Welsh
1. Plants rather strict and often taller, mainly 2–4(–5) dm; fruiting bracteoles, at least some, short stipitate; appendages acute to less commonly acuminate to attenuate; widely distributed.
3. Leaf blades elliptic to oval, attenuate to a cuneate base; sw Colorado, se Utah, and nw New Mexico . . *Atriplex argentea* var. *rydbergii* (Standley) Welsh
3. Leaf blades triangular-ovate to oval, base broadly obtuse to acute or less commonly cuneate; widely distributed.
4. Distal leaves short petiolate; proximalmost leaves alternate; plants mostly less than 4 dm; British Columbia to Manitoba, s through Montana, North Dakota, South Dakota, Wyoming, Nebraska, Idaho, Utah, e Nevada, Colorado, w Kansas, ne Arizona, nw New Mexico . . . *Atriplex argentea* var. *argentea*
4. Distal leaves sessile; proximalmost leaves opposite; plants mostly over 4 dm; California, s Nevada, Arizona, New Mexico, w Oklahoma, w and n Texas . . . . *Atriplex argentea* var. *mohavensis* (M. E. Jones) S. L. Welsh

Atriplex argentea Nuttall var. **mohavensis** (M. E. Jones) S. L. Welsh, comb. nov. Atriplex expansa S. Watson var. mohavensis M. E. Jones, Contr. W. Bot. 11: 20. Protologue type: "Mojave region to San Bernardino, Cal., Jones, Parish." (Paratypes at POM; Parish 1123, 1124 GH!). Type specimen: "*Atriplex expansa* var. *mojavensis* Jones n. var. Mojave, Calif. VIII-26-1894? Collected by Marcus E. Jones A.M.," lectotype (here selected) POM!.

Synonyms. Atriplex expansa S. Watson, Proc. Amer. Acad. 9:116. 1874; *A. argentea* subsp. *expansa* (S. Watson) Hall & Clements, Publ. Carnegie Inst. Wash. 326: 301. 1923; *A. trinervata* (Jepson), Pittonia 2:305. 1982; *A. expansa* var. *trinervata* (Jepson) J. F. Macbride, Contr. Gray Herb. 53: 9. 1918; *A. sordida* Standley, N. Amer. Fl. 21(1): 47. 1916.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

PINUS COULTERI D. Don (PINACEAE).—Santa Cruz County [Ben Lomond Mountain, Santa Cruz Mountains], on private land bounded on NE by Empire Grade [designated "EGS" in following], 37°06'52.5"N, 122°08'28.4"W, growing on crest and SW slope, many hundreds and hundreds of *P. coulteri* of all ages from seedlings to trees of 84 cm dbh, in at least 10 clumps separated from each other by up to 1 km, over area of at least 2 ½ km × 1 km, associated native vegetation includes *Pinus attenuata, Arbutus menziesii, Quercus agrifolia, Quercus wislizenii, Lithocarpus densiflorus, Pseudotsuga menziesii,* occasionally *Pinus ponderosa,* occasionally *Sequoia sempervirens, Ceanothus* spp., *Arctostaphylos* spp., *Rhamnus californica, Eriodictyon californicum, Adenostoma fasciculatum,* access limited by dense undergrowth, including *Toxicodendron diversilobum,* and by broken branches and plant debris (no introduced plants seen), elev. ca. 670–792 m, 25 January 2002; ca. 9 km SE of SE edge of EGS (at power pole 146 on Empire Grade), on private land (5850 Empire Grade), on E side of Empire Grade, 37°02'35"N, 122°06'25"W, some half dozen *P. coulteri* from 2 ½ cm dbh–9 cm dbh (most infected by *Peridermium harknessii*) scattered over area of 75 m × 150 m surrounded mainly by *P. attenuata,* associated species include *P. attenuata* saplings, *Arctostaphylos* spp., *Ceanothus* spp., *Eriodictyon californicum,* and *Toxicodendron diversilobum* (no introduced plants seen), elev. ca. 524 m, 15 March 2002; 1 km from NW edge of EGS, on embankment of W side of Empire Grade, opposite power poles 348–449, 37°07'65"N, 122°10'09"W, single *P. coulteri* 81 cm dbh, with mainly *P. attenuata, Arbutus menziesii, Quercus agrifolia, Lithocarpus densiflorus, Pseudotsuga menziesii,* and *Toxicodendron diversilobum* (no introduced plants seen), elev. ca. 802 m, 25 March 2002.

Previous knowledge. Based on the Vegetation Type Maps (VTM) of California from 1928–1940, J.R. Griffin and W.B. Critchfield (1972. The distribution of forest trees in California. U.S. Dept. of Agric. Forest Service Research Papers PSW 82-1972) mapped the range of *Pinus coulteri* from the Nortonville-Somersville area of Contra Costa County into Baja California.

Significance. First record in Santa Cruz Mountains. Griffin and Critchfield state: "since the VTM survey covered almost the entire California range of Coulter pine, our map is relatively complete" (1972). Neither their map, nor J.H. Thomas' overview (1961. Flora of the Santa Cruz Mountains of California. Stanford, CA), report *P. coulteri* growing in this area. The closest known populations are on Mt. Hamilton (W.L. Jepson 1925. A manual of the flowering plants of California. Berkeley, CA), 53 km distant, and Fremont Peak in the Gabilan Mountain Range (Griffin and Critchfield 1972), 70 km distant.

In 1938 the general area of EGS was classified as "woodland" (H.A. Jensen 1939. Vegetation types and forest conditions of the Santa Cruz Mountains unit of California. Berkeley: California Forest and Range Experiment Station; see VTM). The more common woodland species—various oaks and Pacific madrone—have long been cut as fuel wood in the Santa Cruz Mountains (Jensen 1939), and by 1938 the general area of EGS had been

"deforested" (Jensen 1939; see Timber Resource Map). However, even after considerable harvesting, "sprout growth usually returns [woodland] areas to their former condition within a relatively short period" (Jensen 1939), as has been the case at EGS. Although the site is now virtually undisturbed, localized spots are periodically cleared, and oak and madrone are harvested. In recently cleared areas *P. coulteri* seedlings have established, dominating returning native woodland species. In more mature clumps of *P. coulteri,* smaller specimens are being crowded out by taller members of their own species; the few intermixed trees of other species are about the same height as the tallest *P. coulteri* and seem to be roughly the same age. Apparently these *P. coulteri* germinated in past cleared areas, again dominating native woodland vegetation.

Many of the *P. coulteri* at EGS are at least 50 years old, judging from the large number of cones growing on the branches as opposed to on the bole (cf. Borchert, Madroño 32(1):29–48. 1985). However, presuming an annual diameter growth of 0.45 cm to 1.39 cm (cf. Zobel, Madroño 12:1–7. 1953), the age of the oldest (those of 84 cm dbh) could be anywhere from 60 to 186 years. Since individual trees might have been left when the land was otherwise cleared—e.g., only 50 m from two 84 cm dbh trees a *Q. agrifolia* of 1.27 m dbh was apparently left standing—the oldest trees could indeed be older than the 64 years since deforestation. Did the hundreds of earlier botanists and naturalists who collected and identified plants in the Santa Cruz Mountains as early as 1791 (cf. Thomas 1961) overlook this population? Or has it only been overlooked for the past 50 years? In any event the oversight is probably due in part to the activity of *Sciurus griseus anthonyi* (western gray squirrel): removal of the characteristic cones from trees makes *P. coulteri* more difficult to recognize. Compared to Fremont Peak there are few cones on the trees at EGS but many squirrel-cut cones on the ground.

Was this *P. coulteri* population introduced, or is it native? *Pinus coulteri* was certainly never planted among oaks and madrone as fuel wood. *Pinus coulteri* has no commercial value as a timber tree (A. Farjon and B.T. Styles, 1997. Pinus (Pinaceae). Flora Neotropica 75. 1997) and would in any case never have been planted for lumber in the Santa Cruz Mountains, where redwood and Douglas fir grow naturally and have been commercially lumbered since at least 1841 (cf. Jensen 1939). Could there be some connection with the Christmas tree farm on Empire Grade, directly opposite EGS, where various conifers have been planted since 1948? Even if *P. coulteri* had been planted at that time (*P. coulteri* is not found at the Christmas tree farm today) those trees could not have been the source of the EGS trees. ("Precociously" reproducing *P. coulteri* can bear cones 10 years after germination [cf. Borchert, 1985]; a tree planted in 1948 could have produced seeds at the earliest in 1958; a seed from that tree carried by bird or squirrel to EGS could have reproduced by 1968, making the maximum possible age of EGS trees 34 years.) The seeds are not harvested for consumption (Farjon and Styles 1997), so trees were not planted for that purpose. Although scrub jays are known to feed on *P. coulteri* seeds (R.M. Lanner, 1999. Conifers of California. Los Oli-

vos, CA), it seems unlikely that birds would have flown with seeds from Mt. Hamilton or Fremont Peak. However, since *P. coulteri* seeds were eaten by Indians (P.A. Munz, 1959. A California flora. Berkeley and Los Angeles, CA), they might have carried seeds to the EGS area while hunting deer or while collecting acorns during their "regular seasonal visits to tanbark groves" which were concentrated here (B.L. Gordon, 1996. Monterey Bay area: natural history and cultural imprints. Pacific Grove, CA). Over time, and with the help of squirrels, *P. coulteri* growing from lost seeds could have populated EGS. (The land was classified as deforested after Indians ceased to roam here, but trees now at EGS could be descendants of trees they introduced.)

Perhaps, on the other hand, this *P. coulteri* population was part of the woodland forest at EGS long before Indians could have introduced them. The most compelling argument that a native population continues to assert itself is the natural plant environment in which the trees grow and reproduce. (In terms of the undisturbed condition of the site and the absence of introduced plants, the environment at EGS is more natural, e.g., than that of the native *P. coulteri* population on Fremont peak at approximately the same elevation). The two further sites where *P. coulteri* grows along Empire Grade with native vegetation may indicate that the species was once more widespread in this area. Additional evidence suggesting that the *P. coulteri* population might be native is its proximity to a colony of *Pinus sabiniana* (see documentation below), located 3.8 km NW of the closest *P. coulteri* at EGS (2.7 km NW of the single *P. coulteri*). *Pinus sabiniana* (digger pine, gray pine) is known to grow naturally with *P. coulteri* elsewhere (A. Farjon, 1984. Pines. Leiden; Vale, Madroño 26(3):135–140. 1979); the closest incidence to EGS is in the Gabilan Mountain Range. It is possible that along the Ben Lomond Mountain ridge the two species grow together naturally today, and that they did so in the past.

PINUS SABINIANA Douglas (PINACEAE).—Santa Cruz County [Ben Lomond Mountain, Santa Cruz Mountains], on private land separated by Empire Grade, 37°08′38.75″N, 122°11′50″W, on E side of Empire Grade, N edge of gated entry road below Eagle Rock Lookout, 9 m tall *P. sabiniana*, extending from this tree over area of ca. 800 m², bounded on W by Empire Grade, on S by entry road, 35–40 trees ranging in height from 1–16 m, on grassy meadows otherwise sparsely populated with *Baccharis pilularis, Ceanothus* spp., *Arctostaphylos* spp., *Eriodictyon californicum,* saplings of *Arbutus menziesii* and *Quercus agrifolia,* some *Toxicodendron diversilobum* and an occasional *Pinus attenuata* (which also grows abundantly on surrounding ridges), elev. ca. 679 m; on W side of Empire Grade, on grassy slope N of ranch, over area of at least 100 m², 16 trees up to 20 m tall, elev. ca. 685 m, May 2002.

Previous knowledge. Griffin and Critchfield (1972) show *P. sabiniana* growing throughout most of California.

Significance. First record for Ben Lomond Mountain. Griffin and Critchfield (1972) do not show *P. sabiniana* in this area. Thomas says that in the Santa Cruz Mountains *P. sabiniana* grows only on the Eastern slopes "near Los Gatos, Mount Umunhum, and Loma Prieta Ridge" (1961). How the trees came to be here is uncertain. Some may have been planted for decorative purposes around the ranch and may have spread to the surrounding area. Or, since *P. sabiniana* seeds were a common food for Indians (Lanner 1999), it is possible that the ancestors of these trees were introduced by Indians.

It is also possible that the population is native. This area was grazed by cattle and used for vineyards from ca. 1902 to the mid-1950s (M.R. Holland 1982. Wine history in Santa Cruz County: 1835–present. Senior thesis. University of California, Santa Cruz, CA). In the Gabilan Mountains, where *P. sabiniana* grows naturally, after grazing land was abandoned "the most obvious change in vegetation . . . during the second half of the twentieth century has been the increase in digger pines" (Gordon 1996). Perhaps the same change occurred on this abandoned grazing/vineyard land. Individual trees surviving on the margin of man's activities could have served as the seed-source of a reestablishing native *P. sabiniana* population (growing naturally in proximity to *P. coulteri*). It is pertinent to mention that this general area of the Santa Cruz Mountains is otherwise known for endemic species, including *Arctostaphylos glutinosa, Arctostaphylos andersonii* var. *andersonii,* and *Arctostaphylos silvicola* (Thomas 1961), two stands of *Pinus ponderosa* (Griffin and Critchfield 1972), as well as the rare *Cupressus abramsiana* (Thomas 1961)—only some 200 m from the heavily disturbed land where the *P. sabiniana* population grows. Perhaps *P. coulteri* and *P. sabiniana* are to be added to the list. Voucher specimens for these two species, and a detailed distribution map, have been deposited in the Herbarium at the University of California, Santa Cruz (Museum of Natural History Collections, UCSC). Permission to collect *P. coulteri* specimens from EGS was granted by Ken Kannegard, RMC Pacific Materials.

—KAREN GORDON-GRUBE, 254 Braemoor Dr., Santa Cruz, CA 95060.

CALIFORNIA

DINEBRA RETROFLEXA (Vahl.) Panz. var. *RETROFLEXA* (POACEAE).—Riverside Co., Hemet [Bautista Canyon], Bautista Rd. and Fairview St., 15 Mar 1999, *Riefner 99-162* (RSA) [Det. by J. Travis Columbus, 7 Jun 1999].

Previous knowledge. In a taxonomic revision of *Dinebra* (1973, Kew Bulletin 28:411–418), Phillips indicated that *D. retroflexa* var. *retroflexa,* an annual, is distributed from West Africa east to Sudan and Ethiopia and north to Egypt; Iraq and India. Described as "weedy" by Phillips and "commonly adventive" and "a significant weed species" by Watson and Dallwitz (1994 [rev. ed.], The Grass Genera of the World, CAB International, Wallingford, UK, 1081 pp.), the species has also been documented in eastern North America (North Carolina and Maryland; Kartesz, J.T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland, 1st edition, *in* Kartesz, J.T. and C.A. Meacham. Synthesis of the North American flora [CD rom], ver. 1.0, North Carolina Botanical Garden, Chapel Hill, NC), Europe, China, and Australia.

Significance. First record for California and western North America. Apparently a rare weed, established locally along the edge of a citrus grove. Not encountered during subsequent visits to the area in Jul 1999 and Aug 2003. The presence of *Bouteloua barbata* Lag. in the same area, also as a citrus grove "weed," suggests that *Dinebra* may have been introduced to the present site via grove maintenance equipment used previously in the Coachella Valley region, where *B. barbata* is a common summer annual. Additional occurrences should be sought in the Bautista Canyon region and in other citrus production ar-

eas within southern California, especially the Coachella Valley.

—RICHARD E. RIEFNER JR., J. TRAVIS COLUMBUS, AND STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

CALIFORNIA

SALTUGILIA LATIMERI T.L. Weese & L.A. Johnson (POLEMONIACEAE).—Kern Co. E foothills of Sierra Nevada, just E of Five Fingers, in the drainage of Owens Peak; 1.75 mi, 307.3° (mag.) from Indian Wells; N 35°41′9.6″, W 117°53′28.0″, ca. 3950 ft.; in the shade and on the north side of granite boulders and outcrops. *N. Fraga 638,* (RSA).

Previous knowledge. Saltugilia latimeri was described by Terri Weese and Leigh Johnson in 2001 (Madroño 48: 198–204). The type of this species is from Riverside County, between Whitewater and Morongo Valleys (*V.E. Grant & A.D. Grant 8840*; RSA). The authors noted that this new species is represented by fewer than 20 collections. These collections are from the foothills of the San Bernardino, Little San Bernardino, Santa Rosa, and San Jacinto Mountains (San Bernardino and Riverside Counties); however, two disjunct sites were noted in the Granite/Old Dad Mountains (San Bernardino County; e.g., *E. Jaeger s.n.*; POM) and the Panamint Mountains (Inyo County; *W.L. Jepson 7091*; JEPS).

Significance. The genus *Saltugilia* (A.D. Grant & V.E. Grant) L.A. Johnson is a recently recognized genus of the phlox family (*Aliso* 19: 55–91). This genus includes the former "*Gilia splendens*" group, *Saltugilia grinnellii* (Brand) L.A. Johnson (=*Gilia splendens* H. Mason & A.D. Grant, nom. invalid.), *S. caruifolia* (Abrams) L.A. Johnson, and *S. australis* (H. Mason & A.D. Grant) L.A. Johnson, in addition to *S. latimeri.* This is the first collection of the uncommon Woodland gilia, *S. latimeri,* in Kern County. It is also the first collection of any member of the genus *Saltugilia* from that county. This collection provides a distributional link between the southern populations in the foothills of the San Bernardino, Little San Bernardino, Santa Rosa, and San Jacinto Mountains (ca. 110 mi SW) and the northern location in the Panamint Mountains (43.5 mi. ENE). In addition, it provides evidence that *S. latimeri* occurs on the eastern foothills of the southern Sierra Nevada.

—NAOMI S. FRAGA and J. MARK PORTER, Graduate Program in Botany, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, California 91711.

OREGON

CAREX HARFORDII Mack. (CYPERACEAE).—Coos Co., ditch on margin of cultivated cranberry field, near intersection of Hull Road and Route 101, c. 40 m, T28S R14W S4, 7 Sep 1999, *Zika 14284* (MICH, OSC, WTU; dupl. det. A. A. Reznicek); adventive in sandy cultivated cranberry fields, with *Lotus formosissimus* Greene, *Solidago canadensis* L., ca. 0.5 miles SE of Route 101 on Randolph Road, 1 mile E of Fahys Lake, 55 m, T28S R14W S4, 7 Sep 1999, *Zika 14280* (WTU); CURRY CO., rare adventive in sandy cultivated cranberry fields, with *Lotus formosissimus, Vicia sativa* L., ca. 1.5 air miles SW of Floras Lake, 45 m, T31S R15W S29; 8 Sep 1999, *Zika 14303* (WTU).

Previous knowledge. Harford's sedge was considered restricted to coastal California. Its association with wet ditches in Oregon's commercial cranberry fields is peculiar. Many eastern North American taxa have been introduced as weeds to Oregon cranberry farms by agriculture (Zika 2003, Journal of the Torrey Botanical Society 130: 43–46). Cranberry (*Vaccinium macrocarpon* Aiton) is not cultivated in California, and so it seems unlikely the industry inadvertently introduced *Carex harfordii* to Oregon from California. Perhaps *C. harfordii* colonized the farmed wetlands from adjacent native habitats. Extensive agricultural development may have eliminated most of the native habitat for this species on the southern Oregon coast, and field botanists should search for undisturbed populations of this species.

Significance. First collections for Oregon.

PRUNUS AMERICANA Marshall (ROSACEAE).—Wallowa Co., dense thickets along Little Basin Creek, Dug Bar Road, W side Imnaha River canyon, c. 915 m, T3N R48E S35, 10 Apr 1992, *Zika 11467 & Chambers* (OSC).

Previous knowledge. American plum is native in eastern North America, and has been reported west to Montana and Washington. The Oregon population is small, with fewer than 15 plants, but may be native and disjunct. It is inconspicuous unless flowering.

Significance. First report for Oregon.

ULMUS PROCERA Salisb. (ULMACEAE).—Benton Co., common in thickets, S bank of Marys River, Avery Park, Corvallis, elev. 65 m, 3 Dec 2001, *Zika 16731* (WTU); Jackson Co., several sprouts adventive in shade of *Libocedrus,* Liberty Street, Ashland, 9 Aug 2000, *Zika 15273* (WTU); common in fields, both sides of Eagle Hill Road near I-5, Ashland, 9 Aug 2000, *Zika 15274* (OSC, WTU); same site, fruiting, 28 Apr 2003, *Zika 18288* (OSC, WTU).

Previous knowledge. English elm is native to Europe and occasionally planted as an ornamental in western Oregon. It can spread extensively by root sprouts from planted trees. Vigorous older shoots have characteristic corky wings. It is adventive in California and western Washington.

Significance. First report for Oregon.

WASHINGTON

ATRIPLEX LITTORALIS L. (CHENOPODIACEAE).—San Juan Co., sandy beach near drift logs, Indian Cove, Shaw Island, elev. 2 m, 29 Oct 2001, *Zika 16714* (BRY, WTU).

Previous knowledge. Grass-leaved orache is native to the coasts of eastern North America and Europe. Early reports from Washington by Piper (1906, Flora of the State of Washington) are based on several collections of *A. dioica* Raf. (syn. *A. subspicata* (Nutt.) Rydb.) at WTU. *Atriplex littoralis* is adventive on marine beaches, like *A. prostrata* Boucher ex DC., and found among the native taxa *A. gmelinii* C. A. Mey. ex Bong. (syn. *A. patula* L. var. *obtusa* (Cham.) M. E. Peck) and *A. dioica.*

Significance. First collection for Washington.

BIDENS CONNATA Muhl. ex Willd. (ASTERACEAE).—Clark Co., silty N shore of Columbia River, 1 km W of Oak Park, elev. 5 m, 17 Oct 2002, *Zika 18118* (WTU);

Grays Harbor Co., weed in cultivated cranberry fields, junction Blake and Cranberry Roads, Grayland, elev. 5 m, 19 Oct 1998, *Zika 13652* (WTU); Skamania Co., silty N shore of Columbia River, 2.5 km E of Skamania Island, elev. 8 m, 17 Oct 2002, *Zika 18130* (WTU); Whatcom Co., wetland near cultivated cranberry fields, 0.6 km S of Wiser Lake Road, elev. 24 m, 12 Sep 2002, *Zika 17829* (UBC, WTU).

Previous knowledge. Purple-stem beggarticks is native to eastern North America, west to Nebraska. It has been collected twice in British Columbia as an adventive, and one site was an abandoned cranberry farm (*Lomer 93-241* UBC). It is otherwise unreported from the west coast. The species is essentially rayless and has distinct petioles, but in other respects is similar to *Bidens amplissima* Greene and *B. cernua* L. The warty mature achene faces are easily distinguished from the smooth faces of a similar European adventive in our area, *B. tripartita* L.

Significance. First collections for Washington. Probably introduced by cranberry agriculture to Washington and British Columbia (Zika 2003, *loc. cit.*).

Juglans cinerea L. (JUGLANDACEAE).—Skamania Co., 1 km W of Prindle, fruiting trees common in second growth forest with *Alnus rubra* Bong., *Acer macrophyllum* Pursh, *Thuja plicata* Donn ex D. Don, N side of Route 14, elev. 25 m, 17 Oct 2002, *Zika 18121* (WTU).

Previous knowledge. Butternut is native to eastern North America, west to Minnesota. It is occasionally planted as an ornamental in western Washington.

Significance. First report naturalized in Washington.

Rhamnus cathartica L. (RHAMNACEAE).—Yakima Co., riparian thickets, W shore of Yakima River near arboretum, Yakima, elev. 310 m, 14 Oct 2002, *Zika 18091* (WTU); Sportsman Pond, thickets, E side of Yakima River, near Terrace Heights, elev. 310 m, 14 Oct 2002, *Zika 18096* (WTU).

Previous knowledge. Buckthorn is native to Europe and introduced in eastern North America, west to Montana.

Significance. First collections for Washington.

Rorippa microphylla (Boenn.) Hyl. ex Á. & D. Löve (BRASSICACEAE).—Thurston Co., occasional floating aquatic in sluggish water of Black River, near railroad bridge, SE of Gate, elev. 10 m, 18 Aug 2002, *Zika 17151* (MO, WTU).

Previous knowledge. Narrow-fruited watercress is native to Europe, and a widely scattered adventive across North America, including Oregon and British Columbia.

Significance. First report for Washington.

—Peter F. Zika, Herbarium, Burke Museum, Box 355325, University of Washington, Seattle, WA 98195-5325.

REVIEW

Invasive Plants of California's Wildlands. Edited by CARLA C. BOSSARD, JOHN M. RANDALL AND MARC C. HOSCHOVSKY. 2000. University of California Press, Berkeley, CA. 360 pp. Softcover. $29.95. ISBN 0-520-22546-3.

As ecologists and the general public have become increasingly aware, there are many alien or non-native plant species that have become aggressive invaders in natural plant communities of California. These invasions began more than two centuries ago with the first Spanish missions but have been continuing at an increasing pace with new species introductions. These invaders have had, and are continuing to have, profound ecological impacts on our natural environment in a variety of manners. These include physically crowding out native species by their aggressive growth, altering natural fire frequencies or intensities, changing soil nutrient availability, altering hydrologic stream flow, and competing aggressively with native species for limited soil moisture. Moreover, many of our communities such as grasslands, oak savannas, riparian woodlands, and coastal habitats have been significantly and perhaps irreversibly transformed by invasives. These invasives are not only the cause of significant ecological problems, but additionally produce major economic costs in destruction of productive rangelands, loss of biodiversity, spread of fires, and loss of riparian water resources.

Despite the importance of invasive plant species, there has not previously been a *one-stop* reference to provide both ecological and management information about the most significant invasive species in California. Moreover, much of the available information on individual species and methods for their control has been published in agency reports, sometimes referred to as the *gray literature,* and thus difficult to obtain. The editors of *Invasive Plants of California's Wildlands* are thus to be commended for producing this extremely valuable volume. More than 50 authors contributed to this project.

The book begins with an introduction providing an overview of invasive plant species in wildland habitats of California, followed by a broad discussion of management issues related to invasive plants. These sections provide an excellent background on the environmental issues caused broadly by invasive species in our state and the approaches necessary in considering management programs to control such invasives. Control measures can include physical control as with clearing or fire, biological control, and where appropriate chemical control.

The heart of the book, however, lies with individual short chapters focused on 78 species selected for discussion because of their listing in 1996 as the invasive plants of greatest ecological concern by the California Exotic Pest Plant Council (Cal EPPC). The CalEPPC listing, which includes three categories of increasing concern, was designed not to necessarily list the most common non-native plant species in the state, but rather those species present today which have the greatest potential to cause environmental harm to our state's parks, preserves, and other wildlands. Thus, some readers may be surprised to find that familiar alien plant species such as black mustard (*Brassica nigra*) and wild radish (*Rhaphanus sativus*) are not included. These have little influence on natural plant communities. The focus instead is on the more aggressive invaders, led by such species as giant cane (*Arundo donax*), yellow starthistle (*Centaurea solstitiales*), wild fennel (*Foeniculum vulgare*), and European beach grass (*Ammophila arenaria*) among the 20 species that make the CalEPPC category 1a as the most widespread and aggressive invasives in California. There is much for a reader to learn about not only these widespread invasives, but also about the many other alien species that have more local distributions in the state. Many of this latter group represent plants that need careful monitoring should they begin to expand their range.

A nice feature of the book is the standardization of subheadings within each species chapter. These headings have reader-friendly titles—How do I recognize it? Where would I find it? Where did it come from and how does it spread? What problems does it cause? How does it grow and reproduce? and, How do I get rid of it? Also provided for each species is a listing of common names, other synonyms, and the categories of classification as a noxious weed by both CalEPPC and the California Department of Food and Agriculture. A full set of references is also useful for resource managers and ecologists seeking more information.

Without question, *Invasive Plants of California's Wildlands* is a book that should find its way onto the shelf of anyone concerned about issues of natural resource management, conservation biology, or the environmental biology and natural ecosystems of California. It provides a wealth of core information that will no doubt focus future efforts and lead to an increasing knowledge of these and future invasives in our state.

—PHILIP W. RUNDEL. Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, CA 90095.

PRESIDENT'S REPORT FOR VOLUME 50

As year 2003 comes to a close, I sit here gazing over a beautiful snowy Sierra forest, pondering the end of one cycle and the beginning of another. On reflection, the tenure of Bruce Baldwin as California Botanical Society president during the past three years has been like a super nova of energy and innovation. Under Bruce's watch, *Madroño* publications have quietly gotten back on track, online access to *Madroño* abstracts has enhanced our global audience, two outstanding graduate student meetings have been conducted, a succession of excellent lecture series has taken place, and the society is stronger than ever. On a more subtle level, despite his notable professional status, Bruce has quietly made our society a welcome place, a place where all botanists of whatever stripe are invited to share in the adventure and excitement of our vocation and/or avocation. In short, I want to take this opportunity to celebrate the close of the Bruce Baldwin era as president and to acknowledge the magnificent contribution that he has made to our society. Thank you Bruce!

I'm sure Bruce would be the first to point out that these accomplishments over the past few years would not have been possible without the efforts of several other outstanding members of the California Botanical Society. As your new president, arriving in Fall 2003, it is my responsibility to acknowledge these efforts during this past year. I will do my best to convey the appreciation that I'm sure Bruce would wish to express if he were providing this summary.

At the top of the list must be John Callaway who, as Editor of *Madroño,* has guided our journal through some perilous shoals and heavy seas to a more navigable status, on time and on course. Volume 50 has arrived! Like Bruce, in his quiet and professional way, and with unfailingly good humor, John has shined as the captain of this vessel. Book Editor Jon Keeley, Noteworthy Collections Editors Dieter Wilken and Margriet Weatherwax, and all of the members of the Board of Editors are also to be congratulated, as is former Editor Kristina Schierenbeck who helped get things back on track. *Madroño* is the heart and soul of the California Botanical Society, and it is vital to have it on a sound footing. We owe John and this group of dedicated society members a great debt of gratitude for their impressive efforts.

Another major accomplishment this past year was the annual banquet and 20th graduate student meeting held in San Diego on February 15, 2003. Twenty graduate students presented papers in subjects of paleobotany, ecology, floristics, systematics, and evolution. They represented institutions such as the University of British Columbia, Arizona State University, Rancho Santa Ana Botanic Garden, Claremont Graduate University, UC campuses of Berkeley, Davis, Santa Barbara, Santa Cruz, and Davis, and CSU campuses of Chico and San Diego. First place winners included J. L. Heiser (Arizona State University) for completed research, Rebecca Huft (UC Santa Cruz) for research in progress, and Katrina Duglosch (UC Santa Cruz) for best research proposal. Graduate Student Representatives Robert Lauri of San Diego State University and Elizabeth Zacharias from UC Berkeley were instrumental in organizing the meeting. The evening banquet was highlighted by speaker Jon Rebman from the San Diego Natural History Museum who spoke on the topic of "Discoveries on a Floristic Frontier: Baja California".

Many thanks to everyone who organized and participated in this day long reminder that botany is alive and well in the west!

There have been other important transitions beyond the expiration of Bruce Baldwin's term as president. Another long time Council member, Rod Myatt, retired after three years as First Vice President. Rod did a brilliant job organizing our annual lecture series. We will miss Rod's good humor and organizational talent and extend our sincere thanks for his many years of service. Fortunately, Rod's replacement, Stefania Mambelli of UC Berkeley, has already demonstrated that she also has a talent for organizing outstanding lecture series. Between Rod and Stefania, we have already had outstanding presentations in 2003 by David Ackerly, Kim Steiner, Todd Dawson, and Marcel Rejmanek during the winter/spring series and this fall has included excellent lectures by Walter Koenig, Jeff Corbin, and Gretchen LeBuhn. If you're interested in western botany and biodiversity conservation issues, the UC Berkeley Valley Life Sciences Building is a great place to be every third Thursday evening of the academic year! Thanks to both Rod and Stefania for their excellent efforts. We are looking forward to additional lectures this winter and spring by Michael Loik, Will Russell, Jean Langenheim, and Nishi Rajakaruna. Check out the scheduled lecture topics on our web site (www.calbotsoc.org)!

Our Second Vice President, Michael Mayer, has also left the council. Michael was instrumental in organizing the annual banquet in San Diego. Many thanks for his excellent work. Mark Brunell of the University of Pacific in Stockton has agreed to become Second Vice President. Mark has organized our annual banquet for 2004 at a new and exciting venue, the Presidio of San Francisco, to be held on Saturday, February 21, 2004. The Presidio has played an important part in the rich history of botany in California. It is the type locality for over fifty species of vascular plants, many named during visits by early naturalists in the Spanish and Mexican periods prior to 1848. Today, the Presidio is a flagship representative of the challenges and opportunities for conserving rare plant species and natural habitat remnants under the pressures of contemporary urban environments. Since this is an off year for graduate student meetings, the Presidio Trust staff will host an afternoon tour of Presidio localities to talk about their successful stewardship program. The evening's highlight will be a lecture by Dr. Hal Mooney, an internationally acclaimed physiological ecologist from Stanford University. Hal will speak on "A Personal View of California Plant Ecology: Past, Present, and Future". Please plan on attending this special occasion.

So, I return to my musings: one cycle ends, another begins. Now that our society is on a sound footing, where are we heading? Certainly, a key will be to retain and if necessary replace the talented and dedicated council members who are the unsung heroes of the progress that was made under Bruce Baldwin's presidency. Corresponding Secretary Sue Bainbridge is a perfect example. In my short time in office, it is clear to me that Sue has devoted incredible energy behind the scenes to keeping the society functional. Likewise, Treasurer Roy Buck has worked strenuously to help keep us in the black and to organize our accounting procedures. Recording Secretary Staci

Markos has kept meticulous notes of our council meetings and also done some important work to advance graduate student research in botany. In particular, Staci has focused on launching the Annetta Carter Memorial Fund, an endowed scholarship fund to promote research involving Baja California. Council member Jim Shevock is a fount of energy and inspiration. Council members Dean Kelch and Anne Bradley have also made important contributions. Elizabeth Zacharias has done a wonderful job organizing the social gatherings that take place after our Thursday night lectures in the Jepson Herbarium. Curtis Clark and John LaDuke have done an excellent job launching our web site and will be invaluable in further refining this communication tool. I can only hope that these dedicated individuals will continue to support our efforts or, if changes must be made, help us to find other equally excellent replacements.

We will also have to face the looming retirement of John Callaway as Editor of *Madroño*. We are hoping to build greater support for the editor's function, but it will be vital for us to find someone to carry on John's exemplary efforts. The task will not be easy and I welcome suggestions from society members as to possible candidates. Clearly, now that *Madroño* is back on track, it will be essential for us to maintain our momentum and ideally launch our journal to an even wider audience. In that connection, I hope that all of you continue to renew your memberships in the California Botanical Society and that you encourage your colleagues and institutions to do so as well. Just as *Madroño* is our heart and soul, memberships are our bread and butter!

But all of this begs the question: ultimately, assuming we are able to retain our capacity to function in an optimal manner, where are we heading as a society? Clearly, we must retain our focus on providing a professional voice for the science of botany and related disciplines in western North America. We also must continue to nurture students who will become the professional scientists of future generations. These are central to our core mission. In my view, however, another important role is emerging for our society that perhaps was not envisioned by Willis Lynn Jepson when the California Botanical Society was founded in 1915. This role relates to the important contribution that our society can make to the conservation of biological diversity. We are perilously close to a time when more species are likely to be recognized as extinct than those that are being discovered. Plant species and assemblages are the key to habitat heterogeneity, primary productivity, and biogeochemical processes. These factors are major drivers in the creation and maintenance of biological diversity. As we confront challenges such as global warming and widespread habitat destruction, we need more and better science devoted to habitat restoration, landscape ecology, management of small populations, evaluation of evolutionary relationships, and a host of other related issues.

As we begin this new cycle, it is my personal goal to guide the California Botanical Society in a direction which will reinforce the role that it is already playing in the evolution of botanical science as a major contributor to biodiversity conservation. I welcome your feedback on this goal and I am particularly looking for your help, ideas, and support. Please feel free to email me with your comments at mvasey@sfsu.edu. I hope that everyone enjoys a prosperous and productive new year!

—MICHAEL VASEY
December 2003

EDITOR'S REPORT FOR VOLUME 50

This report serves to inform the members of the California Botanical Society of the status of *Madroño*, from the number of manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 49[4]), the journal has received 58 manuscripts for review (45 Articles and 13 Noteworthy Collections); 13 of these Articles have been accepted for publication in that same time period, along with 12 of the Noteworthy Collections. Additionally, 21 previously submitted manuscripts were also accepted for publication in the last year. The average time for article submission to publication remains at approximately six months. Accepted manuscripts are typically published within approximately three to four months. Few manuscripts were rejected after review; authors of *Madroño* articles did a fine job of responding to reviewers' suggestions.

We have just about reached our goal of getting *Madroño* back to a regular publication schedule. I anticipate that issues 51(1) and (2) will be sent out in early March, and these two issues will put us completely back on schedule. Now that the journal is back on schedule, I hope that the number of submissions for *Madroño* will grow and that we can continue to improve the quality of the journal. Abstracts for *Madroño* are available on-line at the Society's web page (www.calbotsoc.org), as our detailed guidelines for manuscript preparation for *Madroño*. In the near future, we will explore opportunities to expand the level of on-line access to *Madroño*.

I want to thank the many people who have contributed to the publication of *Madroño* over the last year. First, thanks to all of the *Madroño* authors for submitting great manuscripts and being easy to work with in revising and finalizing publications (and thanks for your patience when things sometimes seem to go a little slow). Thanks to the many reviewers who put in a significant amount of time and effort to improve the quality of manuscripts that are published in *Madroño*; I really appreciate the time that reviewers contribute, and I know that authors also are appreciative of your input. Thanks to all of the members of the *Madroño* Board of Editors who provide input on a variety of issues for *Madroño*; special thanks to outgoing members Jon Keeley and Frederick Zechman. Thanks to the members of the California Botanical Society Executive Council who are always extremely helpful and supportive of everything related to *Madroño*. The support of the Council has made it much easier to get the journal back on schedule over the last few years. In addition, the Council has made a substantial effort to increase the awareness and visibility of the Society and *Madroño*, and all of them deserve lots of thanks for their time and effort. Thanks also to Kristina Schierenbeck for her great advice and guidance concerning editorial issues. Thanks to Annielaurie Seifert and her colleagues at Allen Press for their on-going help in bringing *Madroño* to press. Finally, very special thanks to the following people who provide enormous contributions to *Madroño*: Dieter Wilken and Magriet Wetherwax who review all of the manuscripts for Noteworthy Collections, Jon Keeley who coordinates all of the book reviews, and Steve Timbrook who compiles the annual index of *Madroño* articles, as well as the annual table of contents. Without their efforts, *Madroño* would really suffer.

REVIEWERS OF *MADROÑO* MANUSCRIPTS 2003

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ERRATUM

VALIDATION OF *HASTINGSIA BRACTEOSA* VAR. *ATROPURPUREA* (LILIACEAE)

Frank A. Lang
Department of Biology, Southern Oregon University,
Ashland, OR 97520-5071

Peter F. Zika
Herbarium, Burke Museum, Box 355325, University of Washington,
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In an earlier paper (Lang and Zika 1997) we proposed a change of rank for the purple lily endemic to southwestern Oregon, *Hastingsia atropurpurea* Becking (Becking 1986). Our new combination was invalid, as we inadvertently omitted full and direct reference to the date of publication of the basionym (ICBN Art. 33.3; Grueter et al. 2000). Our new combination is validated here.

Hastingsia bracteosa S. Watson var. atropurpurea (Becking) F. A. Lang & P. F. Zika, comb. et stat. nov.

Basionym: *Hastingsia atropurpurea* Becking, Madroño 33:175. 1986.

Literature Cited

Becking, R. W. 1986. *Hastingsia atropurpurea* (Liliaceae: Asphodeleae), a new species from southwestern Oregon. Madroño 33:175–181.

Greuter, W., J. McNeill, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicolson, P. C. Silva, J. E. Skog, P. Trehane, N. J. Turland, and D. L. Hawksworth. 2000. International code of botanical nomenclature (St. Louis code). Koeltz Scientific Books, Königstein, Germany.

Lang, F. A. and P. F. Zika. 1997. A nomenclatural note on *Hastingsia bracteosa* and *Hastingsia atropurpurea* (Liliaceae). Madroño 44:189–192.

ANNOUNCEMENTS

Botany Graduate Students Meet at the University of San Diego

The 20th California Botanical Society Graduate Student Meeting, for students studying any aspect of plant sciences, was hosted by the University of San Diego on 15 February 2003. Robert K. Lauri (San Diego State University) and Elizabeth H. Zacharias (UC Berkeley) planned and organized sessions and oversaw this biennial event where graduate students share their research and ideas in a day of formal talks and discussions with their colleagues. There were 20 abstracts submitted by students from Arizona State University, California State University Chico, Claremont Graduate University, San Diego State University, University of British Columbia, UC Berkeley, UC Davis, UC San Diego, UC Santa Barbara, and UC Santa Cruz. Three morning sessions on Paleobotany, Ecology, and Floristics were followed by two afternoon sessions on Systematics and Evolution, with talks categorized as research that was 1) completed, 2) in progress, or 3) proposed. Rob Lauri chaired all sessions, and graduate students served as judges to evaluate talks in each of the three categories.

Awards for best talks were presented at the annual banquet of the Society, held on campus at the Hahn University Center that evening. First place winners for talks were Jana L. Heisler, Arizona State University (completed—"The interaction of woody vegetation and fire in a C4 grassland: what are the mechanisms driving shrub expansion?"); Rebecca A. Hufft, UC Santa Cruz (in progress— "Genetic and ecological mechanisms of diversification in *Lithophragma* (Saxifragaceae)"); and Katrina M. Dlugosch, UC Santa Cruz (proposed— "The genetics of colonization: native populations vs. recent introductions of *Hypericum canariense,* island endemic to noxious weed"). Second place winners were Vanessa B. Beauchamp, Arizona State University (completed—"Cottonwood-Willow stand structure on regulated and unregulated reaches of the Verde River, Arizona"); Robert K. Lauri, San Diego State University (in progress— "Comparative floristic study of Palomar Mountain State Park"); and Erin K. Espeland, UC Davis (proposed—"Assessing the impact of density, inter- and intra-specific competition on size plasticity in a California annual plant"). Dr. Jon Rebman, Curator of Botany of the San Diego Natural History Museum and renowned expert on the flora of Baja California, gave the banquet address on "Discoveries on a Floristic Frontier: Baja California."

Talks Presented at the 20th California Botanical Society Graduate Student Meeting

Beauchamp, Vanessa B. Department of Plant Biology, Arizona State University, PO Box 871601, Tempe, AZ 85287-1601. COTTONWOOD-WILLOW STAND STRUCTURE ON REGULATED AND UNREGULATED REACHES OF THE VERDE RIVER, ARIZONA. (Completed)

Broughton, Julie D. Department of Geological Sciences, University of California, Santa Barbara, CA 93106-9630. DEAD PLANTS TELL NO LIES; PALEOECOLOGY, PALEOCLIMATE AND PALEOALTITUDE OF THE EARLY MIOCENE MOHAWK VALLEY FLORA, NORTHERN SIERRA NEVADA, CALIFORNIA. (In Progress)

Cummins, Kevin. Department of Biology, San Diego State University, San Diego, CA 92182-4614. SEED BANKS OF LONG-UNBURNED SHRUBLANDS IN CABRILLO NATIONAL MONUMENT. (Completed)

Dlugosch, Katrina M. Department of Ecology and Evolutionary Biology, Earth and Marine Sciences, University of California, Santa Cruz, CA 95064. THE GENETICS OF COLONIZATION: NATIVE POPULATIONS VS. RECENT INTRODUCTIONS OF *HYPERICUM CANARIENSE*, ISLAND ENDEMIC TO NOXIOUS WEED. (Proposed)

Espeland, Erin K. Department of Agronomy & Range Science, University of California, Davis, CA 95616. ASSESSING THE IMPACT OF DENSITY, INTER- AND INTRA-SPECIFIC COMPETITION ON SIZE PLASTICITY IN A CALIFORNIA ANNUAL PLANT. (Proposed)

Fraga, Naomi S. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanic Garden, 1500 North College Ave., Claremont, CA 91711. A VASCULAR FLORA OF THE OWENS PEAK EASTERN WATERSHED. (Proposed)

Griffith, M. Patrick. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, CA 91711. OPUNTIOID CACTUS EVOLUTION AND SYSTEMATICS; INFERENCES FROM DNA SEQUENCE DATA. (In Progress)

Heisler, Jana L. Department of Plant Biology, Arizona State University, Tempe, AZ 85287-1601. THE INTERACTION OF WOODY VEGETATION AND FIRE IN A C4 GRASSLAND:

WHAT ARE THE MECHANISMS DRIVING SHRUB EXPANSION? (Completed)

Honer, Michael A. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanic Garden, 1500 N. College Avenue Claremont, CA 91711. A FLORA OF THE GLASS MOUNTAIN REGION OF MONO COUNTY, CALIFORNIA. (Completed)

Hufft, Rebecca A. Department of Ecology and Evolutionary Biology, Earth and Marine Sciences, University of California, Santa Cruz, CA 95064. GENETIC AND ECOLOGICAL MECHANISMS OF DIVERSIFICATION IN *LITHOPHRAGMA* (SAXIFRAGACEAE). (In Progress)

Igic, Boris. Section of Ecology, Behavior, and Evolution—Division of Biological Sciences, University of California, San Diego, Gilman Drive, La Jolla, CA 92093-5004. THE HISTORY AND CONSEQUENCES OF SELF-INCOMPATIBILITY IN SOLANACEAE. (In Progress)

Kirk, Paul K. Department of Biological Sciences, California State University, Chico, CA 95929-0515. PUTATIVE HYBRIDIZATION OF *JUGLANS HINDSII* IN RIPARIAN FORESTS OF NORTHERN CALIFORNIA. (In Progress)

Lauri, Robert K. Department of Biology, San Diego State University, San Diego, CA 92182-4614. COMPARATIVE FLORISTIC STUDY OF PALOMAR MOUNTAIN STATE PARK. (In Progress)

Miller, Brent S. Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106. MAINTENANCE OF GENETIC VARIABILITY IN POLLEN GROWTH RATES THROUGH POLLEN ATTRITION. (Completed)

Murrell Stevenson, Kathren E. Department of Environmental Horticulture, University of California, One Shields Avenue, Davis CA 95616. ABIOTIC AND PLANT DIVERSITY OF MONTANE MEADOWS IN THE SIERRA NEVADA. (In Progress)

Nettel-Hernanz, Alejandro. Forest Science Division—Department of Environmental Science, Policy & Management, University of California, 145 Mulford Hall, Berkeley CA 94720. COMPARATIVE PHYLOGEOGRAPHY OF WIDE-RANGED MANGROVES IN THE WESTERN HEMISPHERE. (In Progress)

Rajakaruna, Nishanta. Department of Botany, University of British Columbia, Vancouver, BC, Canada V6T 1Z4. EDAPHIC DIFFERENTIATION IN THE *LASTHENIA CALIFORNICA* COMPLEX (ASTERACEAE: HELIANTHEAE): A CASE FOR PARALLEL SPECIATION. (Completed)

Rychener, Tyler J. Department of Plant Biology, Arizona State University, Box 871601, Tempe AZ 85287-1601. STRUCTURAL RESPONSE OF RIPARIAN VEGETATION TO FIRE ALONG THE UPPER SAN PEDRO RIVER, ARIZONA. (In Progress)

Streisfeld, Matthew A. Division of Biological Sciences, University of California, San Diego, 9500 Gilman Dr., La Jolla, CA 92093-0116. MAINTENANCE OF A FLOWER COLOR POLYMORPHISM IN *MIMULUS AURANTIACUS*. (In Progress)

Whittall, Justen B. Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106. PARADOX IN THE FOREST: FLOWER COLOR EVOLUTION IN CONIFEROUS FORESTS OF WESTERN NORTH AMERICA. (In Progress)

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Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

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DEDICATION

Wilfred B. Schofield

Wilfred B. Schofield was introduced to bryophytes by John S. Erskines (a local bryologist) while pursuing a BS degree in botany from Acadia University. After completing his degree in 1950, he taught geology at the high school level. He started working on his master's degree at Stanford University under the guidance of William C. Steere. His taxonomic study of the genus *Hypnum* in Canada and Alaska was completed in 1956. After finishing his Ph.D. under the supervision of Henry J. Oosting at Duke University in 1960, Wilf and his wife Peggy moved back to the west coast when he became an instructor of botany at the University of British Columbia. As a faculty member he was devoted to teaching and working with students. His bryophyte course was very popular and usually filled to capacity. During laboratory sessions fresh bryophyte material and hot tea was always provided for the students to enjoy. Under Wilf's dedicated supervision ten Ph.D. and nine M.S. students successfully completed their degrees. His dedication to teaching was noted when the Faculty of Science awarded him the "Excellence in Teaching" award in 1991–1992.

His primary research interest continues to be phytogeography, and over the years he has published numerous papers on floristics and distributions. Although his focus has been on bryophytes, Wilf is botanically well rounded and knows both vascular plants and lichens. One of the most notable papers demonstrating his botanical expertise, "Phytogeography of northwestern North America; bryophytes and vascular plants," was published in *Madroño* in 1969. Wilf is also well known for his outstanding field collections, and his replicates are in herbaria all over the world. Under his guidance, the University of British Columbia bryophyte collection, through exchanges and his collections, expanded from 2000 specimens in 1960 to well over 250,000 today.

Over the years he has authored several books including: *Some Common Mosses of British Columbia* (1969, 1992 2nd ed.), *Introduction to Bryology* in 1985, and most recently *The Liverwort Genera of Western North America* (2002). His *Introduction to Bryology* was the given the George Lawson Medal by the Canadian Botanical Asso-

ciation for its contribution to Canadian botany. It also was awarded the most distinguished book in life sciences, and the excellence in book design and production by the Professional and Scholarly Division of the Association of American Publishers. He also co-authored four other botany textbooks including: *An Evolutionary Survey of the Plant Kingdom* (1965), *Plant Diversity: An Evolutionary Approach* (1969), *Non-vascular Plants: An Evolutionary Survey* (1982), and *Plants: An Evolutionary Survey* (1984).

Although in 1993, after 33 years of teaching, Wilf officially retired as a full Professor at the University of British Columbia, he continues to come to the office, work extensively in the field, serve on graduate student committees, and publish. He has also inspired and supported numerous bryologists and botanists throughout the world. For additional information on the research contributions that Wilf has made over the years, Volume 82 of the Journal of the Hattori Botanical Laboratory was dedicated to Wilf in 1997 on the occasion of his 70th birthday.

For his distinguished service and continued dedication to bryology, this volume of *Madroño* is dedicated to Wilfred B. Schofield.

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Managing Editor (Name and complete mailing address)

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Date
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